VOLUME LVIII NUMBER 6

THE
BOTANICAL GAZETTE

DECEMBER 1914

THE TRANSPIRATION OF EMERSED WATER PLANTS: ITS MEASUREMENT AND ITS RELATIONSHIPS[1]

CHARLES HERBERT OTIS

(WITH THREE FIGURES AND FOURTEEN CHARTS)

Introduction

The evaporation taking place from free water surfaces has been the subject of much experimentation during the past century, and the laws governing this phenomenon have been quite definitely stated. The matter of transpiration of plants, a special kind of water evaporation, has also been the subject of a great deal of theoretical and experimental investigation, and we know the quantity of water transpired by certain plants in various situations and some of the factors which influence it. But, although the subject is of great importance in regions of small rainfall and scant water supply, especially where immense irrigation and water supply projects are involved, practically no investigation of any importance has been conducted to determine the effect of emersed water plants on the evaporation from a water surface.

It has been a matter of common belief that emersed water plants transpire large amounts of water, although there seems to be little evidence in support of such belief. FANNING (**6**) says, "Marshy margins of ponds are profligate dispensers of vapor to the atmosphere, usually exceeding in this respect the water surfaces themselves." Such statements as this, unsupported by experimental

[1] Contribution no. 143 from the Botanical Department of the University of Michigan.

evidence, are of only passing interest, yet they constitute all of the scanty literature on the subject.

This investigation was undertaken to secure experimental data leading to a better knowledge of the quantity of water transpired by emersed water plants, its relationships, and some of the factors which influence it.

Relation between the amount of water transpired and the amount of water absorbed by the roots

WOODWARD (13) in the latter part of the seventeenth century measured the amount of water absorbed by the roots, and considered this amount to be a measure of the quantity transpired. BESSEY and WOODS (1), in criticism of this method, pointed out that such observations are misleading, that the amount of water absorbed is not necessarily proportional to the amount transpired. Two years later, criticizing a similar mode of reasoning by SCHNEIDER (10), WOODS (12) says, "first of all he has made a very great mistake in assuming that the amount of water absorbed by the roots of a plant represents the amount transpired," and quotes in support of his argument the investigations of EBERDT, BURGERSTEIN, VINES, and GOODALE. WOODS also points out that "transpiration is not something which protoplasm *does* but something which it *resists*. It is not a physiological function or activity of protoplasm, although it may have a physiological relation to the normal development of certain plants or parts of plants. Transpiration is nothing more than evaporation."

BURGERSTEIN (2) reports that VESQUE, using a 0.35 per cent nutritive solution in which bean plants were grown for a period of 56 days, found a water intake of 92.65 gm. and a water outgo of 82.105 gm. He cites also the work of KRÖBER with leafy branches of *Asclepias incarnata*, and shows by the results given in table I that the amount of water taken up by the cut surfaces differs from the amount given off by transpiration.

EWART and REES (5), working with trees, make the statement that "The rate of evaporation per sq. m. of leaf surface from cut branches, whether placed in water or not, is always less than from a plant rooted in the soil, under otherwise similar conditions."

Other recent investigators, among them CLEMENTS (4) and GATES (7), have come to the same conclusion. KRÖBER's results may be criticized, then, on the basis that cut stems and not naturally growing plants were used. It is to be noted, however, that, during the period of the experiment, the amount of water absorbed and the

TABLE I

	Absorption	Transpiration	cc.
9:15 A.M.–6:25 P.M.	11.30	12.80	+1.5
6:25 P.M.–9:50 A.M.	8.05	6.48	−1.57
9:50 A.M.–7:05 P.M.	11.30	11.80	+0.5
7:05 P.M.–7:25 A.M.	7.67	5.21	−2.46

amount transpired were not greatly different, being 38.32 cc. in the one and 36.29 cc. in the other, showing a difference of 2.03 cc. for 42 hours. EBERDT's results with *Helianthus annuus*, as reported by BURGERSTEIN, show even a smaller difference, his figures for a period of 24 hours being as given in table II.

TABLE II

Time	Evaporation of water in cc.	Absorption of water in gm.
7:15 P.M.– 8:45 A.M.	16.67	15.55
8:45 A.M.–11:45 A.M.	4.95	5.53
11:45 A.M.– 3:00 P.M.	5.50	7.40
3:00 P.M.– 7:15 P.M.	6.45	5.50
7:15 P.M.– 7:15 P.M.	33.57	33.98

EBERDT's results, employing the potometer method, are not entirely satisfactory for the reasons stated above. Summarizing the results of these investigations, however, BURGERSTEIN states that if experiments are conducted for periods of 24 hours or longer, using plants that are healthy and under normal conditions for growth and transpiration, and only approximate values are desired, there may be assumed a certain proportionality between water intake and water outgo.

VESQUE (11), experimenting with whole plants subjected to varying physical conditions, comes to the conclusions (1) that the

two functions, absorption and transpiration, are not necessarily proportional; (2) that the absorption is equal to the transpiration when the plant is growing under average and fairly constant conditions, as in diffuse light and in average humidity; (3) that when a plant growing under normal conditions is placed in a dry atmosphere, transpiration is greater than absorption; (4) that when a plant growing under normal conditions is exposed to a saturated atmosphere, the absorption, in obedience to the vacuum already existing, is greater than the transpiration; and (5) that when a plant lacks water, the suction produced by transpiration is not lost, but it accumulates to act immediately when the roots come in contact with water, when absorption is much more energetic than transpiration.

CLEMENTS (4) experimented with potted plants of *Helianthus annuus* and found by careful weighing of the amount of water absorbed by the roots and the amount transpired by the stem and leaves that at the end of 5 days the one equaled the other. His results were as shown in table III.

TABLE III

	Wt. of pot and dry soil	Wt. of pot and wet soil		Total H_2O	H_2O left	H_2O absorbed	H_2O transpired
		I	II				
I.	1846.0 gm.	2218.0 gm.	2174.3 gm.	372.0 gm.	328.3 gm.	43.7 gm.	43.7 gm.
II. . . .	1886.7 gm.	2253.2 gm.	2221.6 gm.	366.5 gm.	334.9 gm.	31.6 gm.	31.6 gm.

To sum up the conclusions of these investigators, the results indicate for land plants growing under natural conditions:

1. That there may be slight discrepancies between the amounts absorbed and transpired if the periods between measurements are separated by a few hours only.

2. That for a longer interval of time between measurements the amount transpired is essentially equal to the amount absorbed.

Hence the amount of water absorbed may be taken as a measure of the amount of water transpired, certainly in view of the fact that any slight error can be scarcely larger than that of any other method applicable to the field. One such error which is known to exist, but which is insignificant when one is dealing with relatively

short periods of time, is the small amount of absorbed water which is used in the building up of plant tissue and also that which becomes a part of the cell sap. Further, since the roots of emersed water plants are constantly in contact with saturated soil, no matter what the transpiration demands, they are never temporarily deprived of water, as may be the case with land plants during periods of excessive transpiration; nor are water plants ordinarily subjected to as great extremes of temperature, relative humidity, and other external factors as are land plants. It is to be concluded, then, that the relations between absorption and transpiration stated above will hold equally well for even short intervals of time, as for 3–4 hours. In the experiments which follow, however, longer periods than this have been chosen, usually of about 12 hours.

Apparatus[2]

The apparatus which was finally adopted consisted essentially of nine large tanks supported in the water by two pontoons. Each tank was equipped with a simple device for measuring the evaporation from the tank. A recording thermometer was housed in a small shelter about 2 m. from the pontoons. Relative humidity was ascertained by means of a cog or "egg-beater" psychrometer (4), which was in each case rested on a support about midway of the vertical height of the growing plants. A barometer of the United States Weather Bureau pattern, but graduated in the metric system, was maintained on shore and read at intervals for the air pressure. Centigrade thermometers for ascertaining the temperature of the water both within and outside the tanks, and graduates of various capacities for measuring the amount of water evaporated were employed. In the experiments conducted on the Huron River at Ann Arbor, a Green's recording anemometer making electrical contact every tenth mile was employed in addition to the apparatus just mentioned. The cups of the anemometer revolved in a plane about 5 dm. above the surface of the water.

[2] An excellent summary describing instruments adapted to the measurement of evaporation from water surfaces is contained in C. F. MARVIN'S Methods and apparatus for the study of evaporation. II. Instruments (9).

The tanks, which were specially constructed for the experiments, were 76 cm. in diameter and 81 cm. in depth, inside measurements (fig. 1). Both cylinder and bottom were constructed of heavy galvanized iron, all joints being well riveted and soldered. A heavy iron band was riveted to the rim, through which were bored four holes, allowing the tank to be supported by spikes driven into the framework of the pontoons. Lighter iron bands were placed at intervals along the length of the tank, to which were riveted internal iron braces, one of which is shown at *a*, fig. 1. The lower edge of the tanks projected about 10 cm. below the bottom. Pieces of wood 5 cm. by 10 cm. in cross-section were fitted into this space and spiked to the projecting sides, as shown in fig. 2. This construction made a tank of great stiffness, which was not easily deformed by rough handling or the tilting caused by wave action, and which produced a solid surface to which the measuring device was secured. The foregoing features were essential, since any deformation of the tank during the progress of the experiments would cause a corresponding change in the volume of the tank and a similar error in the reading.

FIG. 1

The measuring device was a modification of the well known Hooke gauge, and was unique in its simplicity and in the accuracy with which readings could be made. A brass tube of about 6 mm. inside diameter was supported vertically in the center of the tank. The lower end of the tube was threaded and screwed into a socket which was riveted and soldered to the bottom of the tank, while

the upper end terminated in a heavy brass collar. This collar was provided with a socket into which was slipped a solid brass rod, or point, pointed at its upper end. The points were first turned up in a lathe, after which they were placed in a form and ground on an oil stone until a microscopical test showed them all to be of the same angle and of a uniform degree of sharpness. The angle of the cone thus formed was 45°, which was found experimentally to give the best results. Screwed into the sides of the collar at angles of 120° with each other were three iron radius rods terminating in

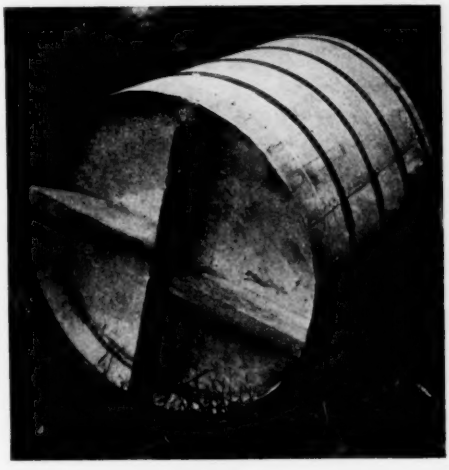


FIG. 2

the heavy iron band at the rim. The outer extremity of the rods was threaded for a considerable distance, so that by means of lock-nuts and rubber gaskets on either side of the heavy band the point could be centered with ease and accuracy. It was essential that the point should be in the exact center of the tank, since only in this position could accurate readings be made in case the tank were tilted slightly from the vertical. The points in all the tanks were set at a distance of 4.5 cm. below the level of the rim.

The pontoons which supported the tanks in the water were at first constructed of rough hemlock lumber and covered with a good grade of asphalt roofing felt. They consisted of two boxes

4.26 m. long, 3 dm. wide, and 3.5 dm. deep. The boxes were left open on the upper side for a greater part of their length to allow a ballast of rocks to be placed to sink the tanks to the required depth. Any water which might enter the pontoons could also be removed through the same opening. It was found to be an advantage to have these pontoons extra large in order that the work of filling the tanks with soil and the placing of plants might be done from the pontoons rather than from a less stable boat. Cross-timbers 5 cm. by 10 cm. in cross-section held the pontoons rigidly

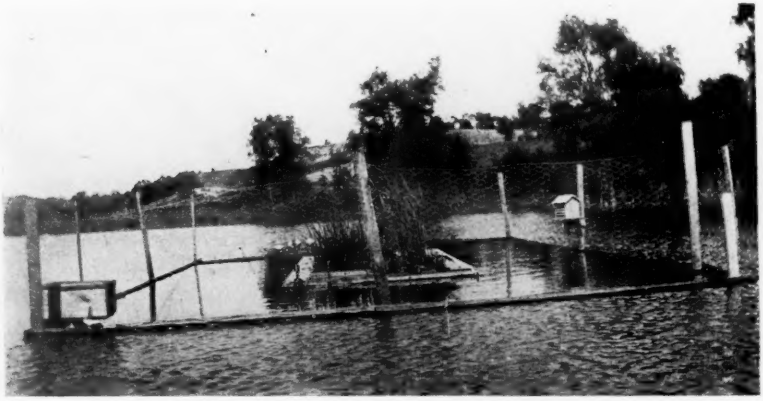


FIG. 3

in place and provided a support for the tanks. It was found necessary to place poultry netting of 5 cm. mesh around the finished raft to a height of 3 dm., and in the horizontal spaces between the tanks, to exclude the turtles which infested the water at this place and which proved rather troublesome. These first pontoons proved to be too frail, since they were easily damaged, with consequent submersion of the entire apparatus. They were replaced the following year by more substantial pontoons with solid tops. The interior of these was subdivided by four water-tight partitions into five compartments. Through holes in the top provided with corks water could be placed in or taken from the compartments, and it was by this means that the proper level of the tanks was

maintained. The wire netting was also removed from the raft, and a netting 1.5 m. high was substituted at a distance of 1.5–2 m. from, but inclosing, the raft, since turtles were not abundant. The relations of the various instruments and the pontoons is shown in fig. 3.

Methods

Readings were regularly made early in the morning and late in the afternoon or early evening, since at these times the water was usually quite still and the light conditions best for accurate readings. A boat was necessary at all times, all work being done from it as soon as observations were begun. Measurements made at the station included wet and dry bulb temperatures as indicated by the psychrometer. Temperatures of the water in the tanks and of the water surrounding the tanks were ascertained and recorded both at the surface and at a depth of 76 cm. beneath the surface. Continuous records of air temperature and wind were made by the recording instruments. The amount of water taken up by the plants or evaporated from the water surface was ascertained by measuring the quantities of water it was necessary to place in the tanks to bring the water to the standard level, as indicated by the height of the point of the brass rod. Water taken from the lake or river surface adjacent to the tanks was always used, since it was of the same temperature and had other characteristics in common with the water in the tanks. Once a week the tanks were filled to overflowing with several bucketfuls of water rapidly applied to remove any scum or refuse matter which might accumulate and which would influence the evaporation therefrom.

The best way to ascertain accurately the amount of water to be added to a tank in each case was found to consist in adding a little more water than was necessary to cover the point. On placing the eye close to the level of the water a point could be found where the entire surface of the water in the tank appeared like a bright mirror. Then, with the eye directed toward the center of the surface, a small quantity of water was removed. As soon as the surface became still, an examination was made for the appearance of the point. If it did not show, more water was removed, until finally a minute black spot was distinguishable in the center of the

mirrored surface. (If, at this stage, more water is removed, the minute spot rapidly enlarges, spreading out in a circle around the exposed point.) A very small quantity of water was then added, just enough to obliterate entirely the dark spot. Usually the finger was applied to the point at this stage, a slight rubbing serving to clean the point and to break the surface film of the water over the point. The point was shown to be just beneath the surface, as, on lightly touching the water with the finger, a tiny wave would be sent across the surface, and the point would appear momentarily to be immediately obliterated. This phenomenon was most readily observed when the light was somewhat diminished. At midday the sun on a cloudless day was so intense that the eye was flooded with the light reflected from the water surface, making it difficult to see the dark spot. Repeated observations under varying conditions carried out with a test tank showed that on the average a change in water height produced by the addition or subtraction of 25 cc. of water could be detected. Since the area of water surface in the tank approximated 4,575 sq. cm., this volume would give a theoretical difference in height, or minimum error due to observation, of 0.05 mm.

Experiments

Experimental stations were established and maintained during the summers of 1910 and 1911. The first was located in a bay of about 12 hectares' extent in Portage Lake, situated 27 km. northwest of Ann Arbor, Michigan. A long, narrow peninsula covered with a scrubby growth of trees and shrubs separated the bay from the lake proper and protected the station from the prevailing westerly winds. It was subsequently found necessary to establish a boom of floating logs on the south and east as a protection against occasional winds from these directions.

Two tanks at the diagonal corners of the raft contained neither soil nor plants and were used to ascertain the evaporation from the free water surface. The other tanks were supplied with lake mud, the depth depending upon the plants placed therein. Plants from the immediate vicinity were planted in these tanks, the depth of the water being in all cases identical with the depth of the water where the plants were naturally growing. Care was also taken to set the

plants as nearly as possible in the same density of stand as naturally growing plants in the lake. Where there was any tendency for the plants to work their way out of the soil, which was of common occurrence among the larger kinds, on account of their natural buoyancy and the extreme looseness of the newly placed soil, stones were used freely to press down the roots and hold them in place. The plants used during 1910 were *Scirpus validus* and *S. americanus*, *Sagittaria latifolia*, *Castalia odorata*, *Pontederia cordata*, *Typha latifolia*, *Zizania aquatica*, and *Eichhornia speciosa*. The two latter were discontinued before the measurements were begun, as the *Zizania* was twice completely destroyed by water animals and the *Eichhornia* floated away the first time the raft sank. The plants, after transplanting, were allowed to remain undisturbed for a period of two weeks, during which time they became well established.

At the beginning of the experiment measurements were made of the area of leaf and stem surfaces exposed to the action of the air. These measurements were made in the following manner. In the case of those species having petioles and expanded blades (as *Sagittaria* and *Pontederia*), a tracing was made of every leaf blade or portion of a leaf blade above the standard water level, and the upper and lower diameters and length of the petioles above water were recorded separately. Subsequently the area of blade surface was ascertained by use of a planimeter and the area of petiole surface was calculated as the area of the frustum of a cone. In the case of *Scirpus validus* the height of the culm above the water and its basal diameter were recorded, its surface being calculated as the surface of a cone having the dimensions recorded. With *Scirpus americanus* similar measurements were made, the surface being treated as the surface of a pyramid whose base is an equilateral triangle. The leaves of *Typha* were measured for the length exposed to the air (not the height above the water) and the width of the corresponding base, the surface exposed being calculated by treating each leaf as a triangle whose base is the width and whose altitude is the length given. Finally, a photograph of the surface of the tank containing *Castalia* was made from a point exactly above the center of the tank, since leaf tracings of the

floating leaves could not be made without injuring them. By means of the planimeter and a simple proportion the surface of the leaves exposed was approximated. During the course of the experiment, when leaves or parts of plants were for any reason removed, the parts were measured and a record was made of the date of removal. At the end of the experimental period all parts above water were again measured and calculated in the same manner as outlined above. In making calculations the slide rule was resorted to wherever practicable.

A second station was established in the summer of 1911 in the Huron River near Ann Arbor. The river at this place is about 60 m. wide. There is little or no natural protection on any side, and it was necessary to inclose the entire station by a stationary boom. The plants were in this case taken from the river near by. They included *Scirpus validus*, *Typha latifolia*, *Castalia odorata*, and *Pontederia cordata* used the first year, together with *Sparganium eurycarpum* and *Acorus Calamus*. Owing to the withdrawal of the water for a period of several weeks, while repairs were being made on a near-by dam, the *Sagittaria latifolia* was all but destroyed and could not be used. Consequently only eight tanks were used. Two tanks were used as controls and the preliminary treatment of the plants was the same as at the Portage Lake station. The plants were not measured, however, and the surface area exposed to the air was not ascertained.

Just before measuring observations were begun, pontoons and tanks were sunk to such a depth that the water in the tanks and the water of the lake were in the same horizontal plane, which was 4.5 cm. below the level of the rim.

Ecological and physiological aspects of plants used

1. *Scirpus validus* Vahl. (great bulrush) inhabits the still water at the margins of lakes, ponds, and quiet streams, or covers shallow shoals in lakes, often forming thick stands of large extent. The maximum depth of water in which good growth occurs is about a meter, while the denser stands are found in depths of 3–6 dm. The culms are stout, terete, attaining a height of 2.5 m. under

favorable conditions, and rising stiffly above the water or bending in graceful curves. The leaves are reduced to basal sheaths. Seed is usually abundant, while vegetative propagation is secured by perennial, creeping rootstocks.

2. *Scirpus americanus* Pers. (three-square or chair-maker's rush) inhabits the borders of lakes, ponds, and streams, usually in water somewhat shallower than the great bulrush. It does not form thick stands, as does the latter, but is sparingly placed here and there. The culms are sharply three-angled throughout, with concave sides, growing straight upward, sometimes twisted or curved, to a height of a meter. The leaves are basal, narrowly linear, 1–3 dm. long, usually not appearing above the water. The rootstocks are long, stout, perennial.

3. *Pontederia cordata* L. (pickerel-weed) inhabits the shallow water of lakes, ponds, and quiet streams, making its best growth in depths of 2–3 dm. The plants usually stand in clumps, sending up several erect, long-petioled leaves and spikes of showy, blue flowers to a height of 6–12 dm. The leaf blades are ovate to cordate-sagittate, 1–2 dm. long, and about one-half as wide at the base. Stomata occur plentifully on the petioles and both sides of the leaves, but they are somewhat more numerous on the lower than on the upper sides of the blades. Propagation is secured by an abundance of seed, but chiefly by thick, creeping, perennial rootstocks.

4. *Sagittaria latifolia* Willd. (arrow-head) inhabits only the shallowest water and muddy banks of lakes, ponds, and rivers, usually in solitary clumps and seldom covering any considerable area. The leaves are basal, long-petioled, arising from tuberous or fibrous rootstocks to a height of 6 dm. or more. The leaf blades vary greatly in size and shape, but they are nearly always sagittate. Stomata occur sparingly on the upper surface of the blade and on the petiole, but are only moderately abundant beneath.

5. *Acorus Calamus* L. (sweet flag) is rather infrequently found along the margins of streams in water as much as 4–6 dm. in depth. The narrow, sweet-scented, swordlike leaves arise from the thick,

creeping rootstocks to a height of 6 dm. to a meter or more, often forming dense stands over small areas.

6. *Sparganium eurycarpum* Engelm. (bur-reed) inhabits water 4–6 dm. in depth on the borders of ponds, lakes, and rivers, rising to a height of 8–15 dm. The leaves are linear, mostly flat. While propagation is provided vegetatively by perennial, creeping rootstocks, solid stands of any considerable area are exceptional, growth in small groups being usual.

7. *Typha latifolia* L. (common cat-tail) inhabits the marshy banks and shallow water of marshes, lakes, and rivers. The leaves are linear, flat, sheathing at the base, commonly growing to a height of 1–2 m. The plants usually stand in close clumps and sometimes predominate over a considerable area. Stomata are abundant on both sides of the leaves. Propagation is by perennial, creeping rootstocks.

8. *Castalia odorata* (Ait.) Woodville and Wood (sweet-scented water lily) inhabits water of varying depths, covering large areas in shallow ponds and the still water of lakes and slow streams, or mingling freely with open-growing forms of water plants, even occupying the deeper water to the exclusion of other plants when crowded out by competition. The large rootstocks creep through the soft mud, sending up large leaves at the end of long petioles and large, showy, white flowers. The leaves are 0.5–2 dm. wide, orbicular, and float on the surface of the water, frequently partly covering one another in the struggle for space. Stomata occur on the upper side only, but here they are very numerous and their openings are relatively wide. The stomata are kept free from water in the following manner. KERNER (**8**) states that the leaves are slightly raised where they join the petiole and the margins are somewhat undulating up and down, so that any water which may find itself thereon will roll down from the center of the leaf to the edge on the slightest rocking movement, where it coalesces with the water on which the leaves float. The under side of the leaves is often colored purple by anthocyanin, by virtue of which the temperature of the leaves is said to be raised somewhat above that of the water, tending to increase the transpiration therefrom.

Results

EVAPORATION FROM A FREE WATER SURFACE AND FROM A WATER SURFACE OCCUPIED BY EMERSED WATER PLANTS

A compilation of the data collected during the summers of 1910 and 1911 shows a number of features of interest concerning the evaporation from water surfaces. As would be expected from a consideration of the various plants used, their differences of growth, habit, and structure, together with the varying physical factors, the results show considerable diversity in total and relative amounts of evaporation. A vast amount of data has been recorded throughout the course of the investigation, all of which it is impossible to include in this paper. The statistical tables and graphs which are published here for the most part summarize the more detailed data. The results fall naturally into several groups, which will be taken up successively.

(*a*) *Total amount of water evaporated*

Tables IV and V give in tabular form the amount of water added to each tank, which represents the amount of water evaporated by water and plant surfaces during any period, for successive intervals. It will be noted that the total amount of water added varies over a considerable range for the different tanks. If the average of the two control tanks be accepted as the amount of evaporation from a free water surface, to which a value of 1 is assigned, then the plants used in 1910 would stand in order of evaporating power thus: pickerel-weed:cat-tail:arrow-head:great bulrush:three-square rush:water lily as 1.98:1.88:1.55:1.19:1.12:0.86. Using the plant combination indicated in table V, the ratio would appear as follows: cat-tail:sweet flag:bur-reed:pickerel-weed:great bulrush:water lily as 3.05:2.36:2.26:2.08:1.20:0.89. The values for water lily (0.86 and 0.89) and for great bulrush (1.19 and 1.20) are nearly the same for the two years. The other values are much higher for 1911, thought to be due in part to the somewhat drier season and more exposed situation and in part to a more luxuriant growth. The evaporation from the water lily tank was in both years much less than that

from the control tanks. This might be expected from the fact that the lily leaves floated on the water, forming a partial cover and reducing the area of water surface exposed to the air. Moreover, lying in a plane only slightly above that of the water surface itself, the lily leaves were constantly bathed by the very humid atmosphere which is commonly present a short distance above the water surface. It is also probable that the amounts assigned to the taller-growing plants are somewhat lower than the actual, since dew collected heavily on the cooler and broader leaf surfaces during foggy nights and, running down the veins and petioles, found its way into the tanks, thus making the observed measurement too small. The water lily was the only plant found to diminish the evaporation from a water surface. All other plants, especially those with a large leaf and petiole surface exposed to the air, increased the evaporation, in one case as much as three times (for example, cat-tail, table V).

(*b*) *Periodicity of evaporation*

Referring again to tables IV and V of comparative evaporation, it will be noticed that a comparison of successive day and night records for any one tank usually shows a period of high rate of evaporation during the day, followed by a relatively low rate of evaporation during the succeeding night. This phenomenon is most conspicuous in the cat-tail, sweet flag, pickerel-weed, and others exposing a large transpiration surface to the air, and least evident in the rushes and water lily.

The amounts of evaporation from the various tanks given in tables IV and V have been incorporated for the sake of convenience and ready comparison in charts I–XIV, the standard of comparison being the rate of evaporation in cubic centimeters per hour. Charts I and VIII show the rate from the control tanks, and the mean value has been taken to represent the rate of evaporation from a free water surface. These values are plotted in the graphs of charts II–VII and IX–XIV with a heavy broken line. The heavy solid line represents the rate from the tanks containing emersed water plants, that is, the evaporation from the water surface of the tank plus the evaporation from the plant surfaces. The vertical

distance between the horizontal lines representing the evaporation from the free water surface and that from the water surface and plant surface together represents the evaporation due to the plant surfaces alone.

TABLE IV

COMPARATIVE EVAPORATION IN 1910

DATE	APPROX. TIME INTERVAL IN HRS.	CONDITIONS	AMOUNTS OF EVAPORATION FROM THE TANKS (CC. OF WATER ADDED)							
			Arrow-head	Three-square rush	Pickerel-weed	Cat-tail	Water lily	Great bulrush	Control no. 5	Control no. 2
Aug. 10..	6	Day	834	519	1400	1200	470	550	450	400
10..	18	Day and night	1650	1400	1715	1750	1015	1425	1150	1375
11..	12	Day	1750	1250	2400	2250	1215	1250	1300	1100
11..	12	Night	1150	1030	987	1053	750	1090	975	1100
12..	10	Day	1600	975	2585	2650	900	1080	1140	750
12..	14	Night	1500	1575	1300	1250	990	1550	1225	1570
13..	11	Day	1770	975	2490	2385	975	1150	790	660
13..	13	Night	988	940	1000	1193	630	1000	910	1120
14..	10	Day	1730	995	2425	2445	905	1090	835	762
14..	14	Night	745	750	887	820	475	730	715	767
15..	8	Day	1145	500	1845	1840	575	673	500	407
16..	9	Day	940	553	1247	1245	450	610	452	425
16..	14	Night	650	553	654	650	420	600	500	500
17..	10	Day	1495	815	2060	1785	630	863	580	678
19..	11	Day	2070	1317	2890	2673	1185	1550	1340	1130
19..	13	Night	1305	1300	1398	1358	863	1327	1228	1250
20..	11	Day	2058	1235	2670	2565	970	1405	1000	1063
20..	23	Night and day	2950	2150	3728	3378	1435	2063	1837	1913
21..	12	Night	783	685	890	900	395	785	655	595
26..	25	Day and night	2920	2075	3470	3255	1675	2175	1725	1918
27..	7	Day	1042	575	1590	1500	555	805	543	460
27..	13	Night	955	950	925	865	590	850	860	990
28..	25	Day and night	2755	2070	3660	3375	1587	2180	2100	1395
29..	10	Day	2267	1443	3040	2587	810	1550	958	1040
29..	13	Night	1080	975	1305	1235	650	1055	1045	905
Totals for an approximate period of 324 hours (cc. of water added)			38,132	27,605	48,561	46,207	21,115	29,406	24,813	24,273

In most instances the evaporation during the night was found to be in excess of that from the free water surface, indicating that emersed water plants transpire during the night. An exception is the case of the water lily, in which the evaporation was usually

less than from the free water surface. We are led, then, to the conclusion that transpiration from these plant surfaces occurs both by day and by night, but that the day transpiration is greatly in excess of that taking place at night. These observations are

TABLE V

COMPARATIVE EVAPORATION IN 1911

DATE	APPROX. TIME INTERVAL IN HRS.	CONDITIONS	AMOUNTS OF EVAPORATION FROM THE TANKS (CC. OF WATER ADDED)							
			Cat-tail	Sweet flag	Pickerel-weed	Bur-reed	Great bulrush	Water lily	Control no. 8	Control no. 1
Aug. 30..	12	Day	4160	3590	2860	3085	1630	1175	1095	1420
30..	12	Night	1000	780	680	1145	680	620	600	615
31..	12	Day	3050	2405	1905	2100	745	490	585	510
31..	12	Night	600	540	560	520	595	520	575	575
Sept. 1..	11	Day	5110	3410	3200	3360	1300	790	950	835
1..	13	Night	925	860	870	800	660	455	575	655
2..	24	Day and night	7560	5730	5075	5725	3120	2310	2780	2880
3..	12	Day	4850	4300	3090	3945	1960	1415	1545	1690
3..	12	Night	1050	935	920	975	1030	830	830	1030
4..	11	Day	5680	4200	4060	3540	1880	1345	1270	1550
4..	12	Night	780	730	640	725	710	630	655	720
8..	8	Day	1885	1495	1885	1250	400	265	255	265
8..	14	Night	440	375	340	380	240	210	225	250
9..	10	Day	3240	2285	1915	2250	580	350	360	350
9..	13	Night	640	580	400	530	510	465	510	600
10..	9	Day	3030	2025	1735	1940	535	300	365	345
10..	15	Night	550	460	210	440	270	175	220	240
13..	11	Day	4640	3620	2800	3450	1700	1130	1180	1390
13..	13	Night	1430	1240	1220	1280	1195	1030	1050	1180
15..	8	Day	3880	2275	2425	2570	700	485	530	440
15..	13	Night	700	655	575	740	510	430	380	470
19..	13	Night	1500	1360	1285	1250	1350	1120	1200	1330
Totals for an approximate period of 270 hours (cc. of water added)			56,700	43,850	38,650	42,000	22,300	16,540	17,735	19,340

in accordance with the results obtained by CLAPP (3) and others with land plants, in which it has been found that land plants transpire principally during the day and only feebly if at all at night.

(c) *Relation of transpiration to transpiring surface*

It has been commonly held, for land plants at least, that with plants of different species, or even with different plants of the same species, there is no relation between the amount of water tran-

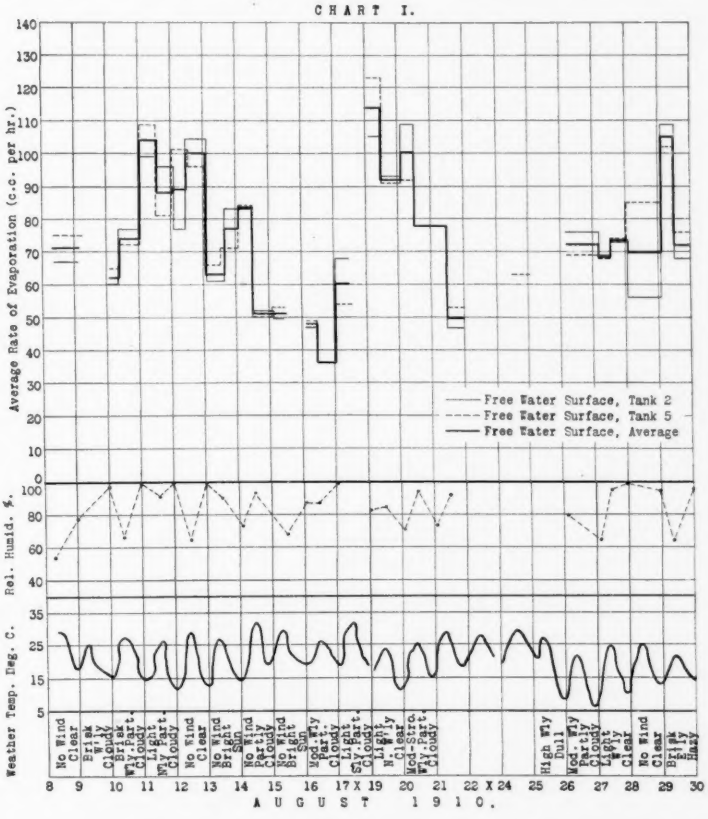
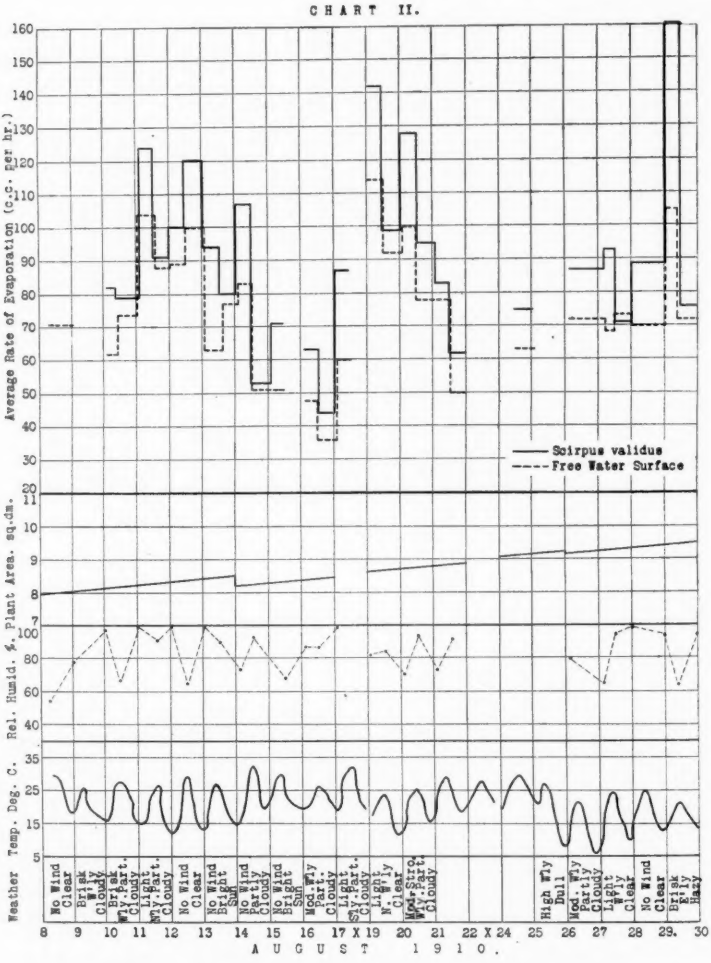


CHART I.
Average Rate of Evaporation (c.c. per hr.)
Free Water Surface, Tank 2
Free Water Surface, Tank 5
Free Water Surface, Average
Rel. Humid. %.
Weather Temp. Deg. C.
No Wind Clear
Brisk W'ly Clear
W'ly Part. Cloudy
Light W'ly Part. Cloudy
No Wind Clear
No Wind Bright Sun
No Wind Cloudy
No Wind Bright
Mod. W'ly Part. Cloudy
Lt. Part. Cloudy
Light W'ly Clear
Mod-Stro. W'ly Part. Cloudy
High W'ly Dull
Mod. W'ly Cloudy
Light W'ly Clear
No Wind Clear
Brisk W'ly Hazy
8 9 10 11 12 13 14 15 16 17 X 19 20 21 22 X 24 25 26 27 28 29 30
AUGUST 1910.

spired and the area of the transpiring surface exposed to the air. Dealing collectively with a number of plants of the same species, so that an average transpiration rate overcoming individual differences was obtained, this fact was borne out in the experiments of 1910. Utilizing the data on the amount of plant surface exposed

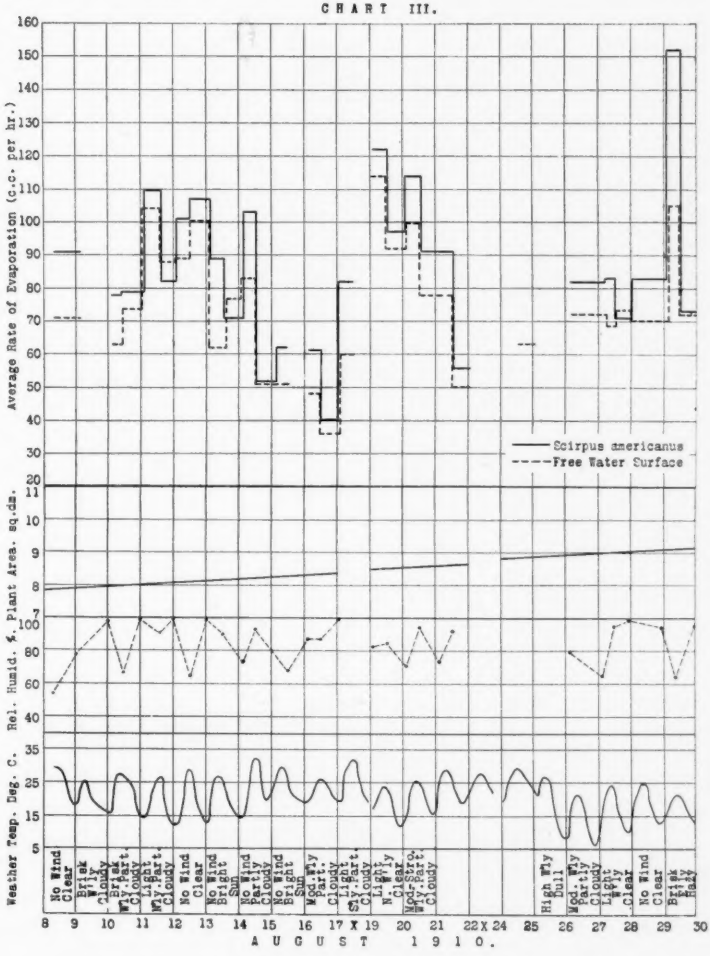
to the air, described under the heading "Experiments," the growth curves of charts II–VII were constructed as a working basis for



the transpiring surface. Growth in area was assumed to be uniform from the time of starting the readings to the date of final measurement, making due allowance for the loss of surface oc-

casioned by the removal of the various parts from time to time. This was thought to approximate very nearly growth under normal

CHART III.


Average Rate of Evaporation (c.c. per hr.)
Scirpus americanus
Free Water Surface
Rel. Humid. & Plant Area. sq.dm.
Weather Temp. Deg. C.
No Wind Clear
Brisk Mly Cloudy
Brisk Mly Part. Cloudy
Light Mly Part. Cloudy
No Wind Clear
No Wind Bright Sun
No Wind Partly Cloudy
No Wind Bright Sun
Mod.Mly Part. Cloudy
Sly.Part. Cloudy
Light Clear
Mod.Str. Mly Part. Cloudy
High Mly Dull
Mod.Mly Cloudy
Light Mly Clear
No Wind Clear
Brisk Mly Rain
8 9 10 11 12 13 14 15 16 17 X 19 20 21 22 X 24 25 26 27 28 29 30
AUGUST 1910.

conditions of development. Both sides of the leaf blades, with the exception of those of the water lily, which contain stomata on the upper side only, and those portions of the petioles or culms above

the level of the water surface were taken as a basis for transpiring surface, since these surfaces all contained stomata in greater or lesser numbers. The unit of surface selected was, for convenience, the square decimeter.

Table VI shows the rate of transpiration in cc. per hour per sq. dm. of total plant surface. Several things are brought out. The rate during the day is usually much higher than the night rate. This is not so apparent in the case of the water lily, for in this instance the difference between day and night rates is not so great as in the other cases. This is remarkable when it is considered that the lily leaves float on the surface of the water in a very humid atmosphere, especially at night, whereas the taller-growing plants are in a relatively less humid layer of air. This may be accounted for in part by the fact that the lily leaves, because of their contact with the water, are warmer at night than those leaves which project into the air, which is much cooler than the water during most of the nights.

TABLE VI

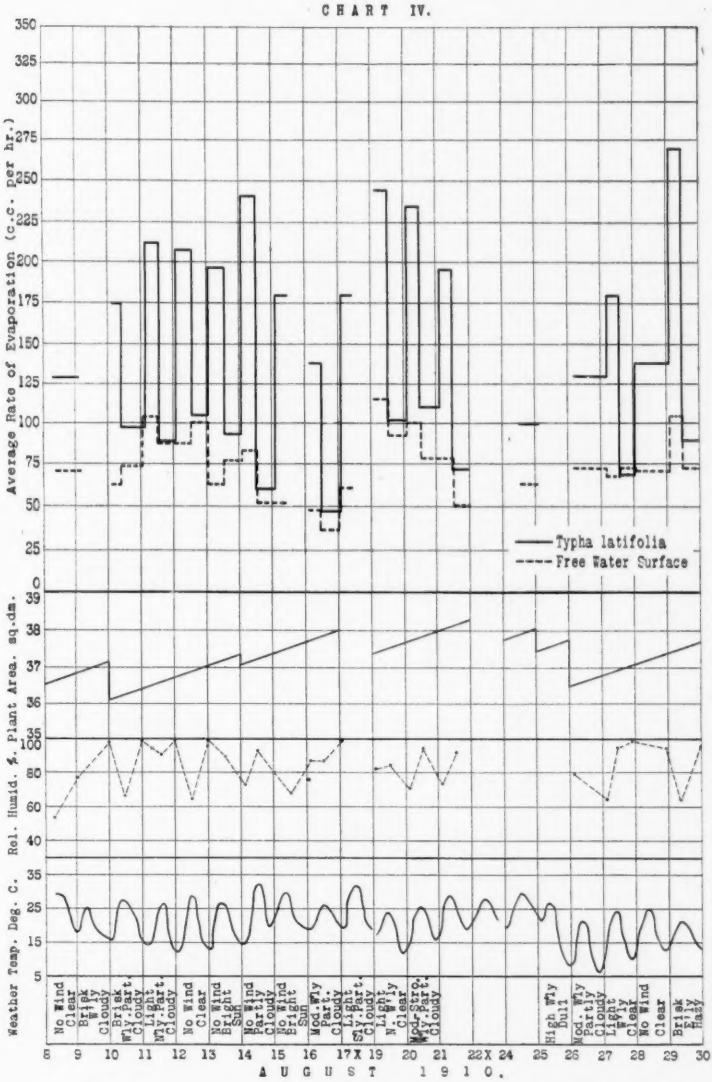
RATE OF TRANSPIRATION PER AREA OF SURFACE

DATE 1910	CONDITIONS	TRANSPIRATION IN CC. PER HOUR PER SQ. DM. OF TOTAL PLANT SURFACE						
		Pickerel-weed	Cat-tail	Arrow-head	Great bulrush	Three-square rush	Water lily	Free water
Aug. 10..	Day	1.758	1.565	0.718	2.463	2.007	1.704	1.359
10..	Day and night	0.274	0.332	0.224	0.616	0.627	1.184	1.623
11..	Day	1.654	1.483	0.501	2.439	0.750	2.280	2.281
11..	Night	.....	0.000	0.044	0.366	.....	1.125	1.929
12..	Day	1.603	1.608	0.827	1.325	1.481	1.799	1.952
12..	Night	0.060	0.054	0.056	2.409	0.864	1.428	2.193
13..	Day	1.696	1.797	1.045	3.690	3.198	2.017	1.381
13..	Night	0.012	0.216	.....	0.357	.....	0.811	1.688
14..	Day	1.812	2.129	1.050	2.927	2.439	2.119	1.820
14..	Night	0.140	0.108	0.011	0.244	0.122	0.579	1.118
15..	Day	1.665	1.885	0.920	2.409	1.333	1.647	1.118
16..	Day	0.872	1.194	0.613	1.789	1.566	1.083	1.053
16..	Night	0.172	0.146	0.120	0.954	0.482	0.605	0.789
17..	Day	1.670	1.566	0.982	3.187	2.631	1.407	1.316

Aside from these differences between day and night rates of transpiration, there is also a great difference between the rates from different species during the same time period. Again, the

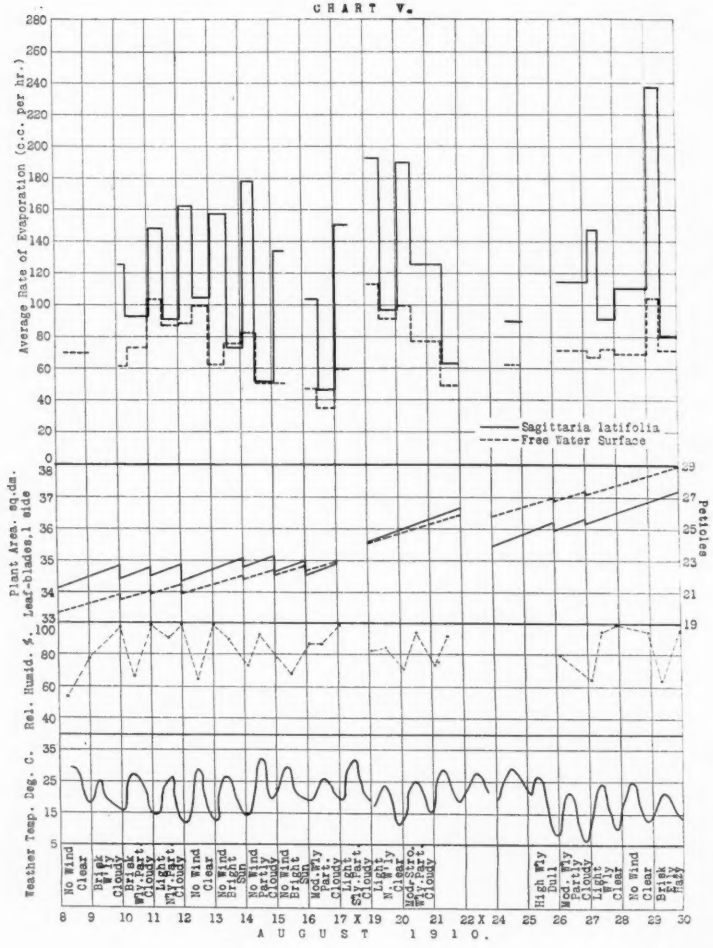
difference is not so marked in the case of the night readings, but is conspicuous during the day. On a basis of surface exposed, the

CHART IV.


Average Rate of Evaporation (c.c. per hr.)
Typha latifolia
Free Water Surface
Plant Area. sq.dm.
Rel. Humid. %.
Weather Temp. Deg. C.
No Wind Clear
Brisk Wty Cloudy
Light Wty Cloudy
Wty Part. Cloudy
No Wind Clear
No Wind Bright
No Wind Partly Cloudy
Eo Wind Part Sun
Mod. Wty Part. Cloudy
Sly. Part. Cloudy
Light Wty Clear
Mod. Stro. Wty Part. Cloudy
High Wty Dust
Mod. Wty Partly Cloudy
Light Wty Clear
No Wind Clear
Brisk Wty Hazy
5 6 7 8 9 10 11 12 13 14 15 16 17 X 19 20 21 22 X 24 25 26 27 28 29 30
AUGUST 1910.

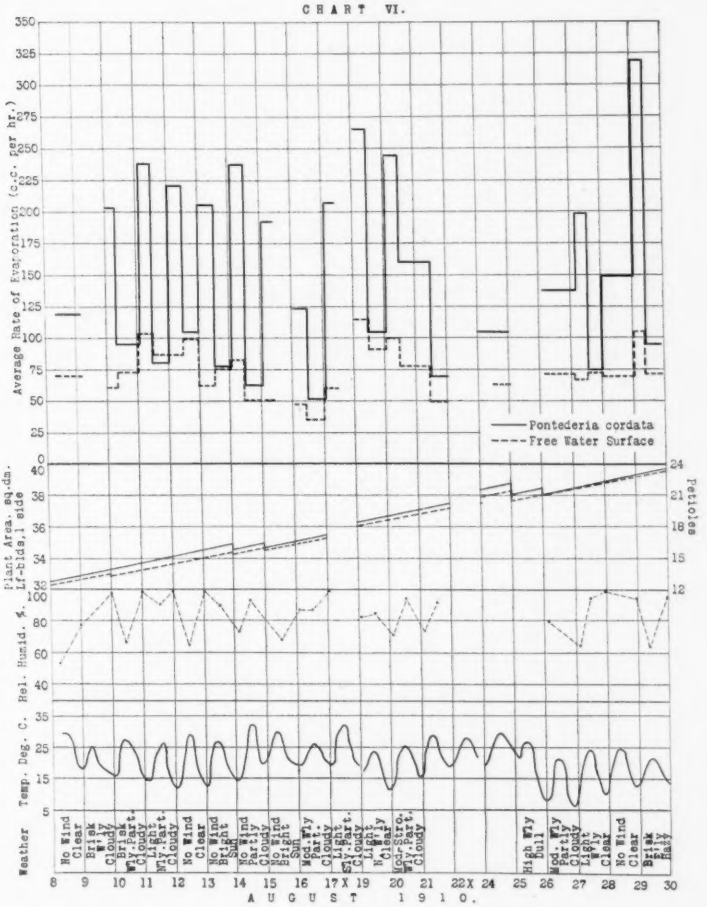
arrow-head would seem to be the least effective from the standpoint of water dispersal, the rushes and water lily showing greatest efficiency, with the pickerel-weed and cat-tail occupying an inter-

mediate position. GATES (7), with a temperature of 26° C. and a relative humidity of 69 per cent, reports that cuttings of *Sagittaria*



latifolia had a rate of water conductivity of 49 cm. per hour, while cuttings of *Typha latifolia* had a rate of 114 cm. per hour. It should be remembered, too, that in the case of the cat-tail all of the

stomatal surface is not equally effective, owing to the sheathing habit and consequent crowding of the leaves, while in the pickerel-weed and arrow-head a similar decrease in transpiration is caused



by shading and by hindrance to air movements by the closely growing leaves and petioles. This might explain in a measure, or at least have some influence on, the differences in transpiration rates for different species.

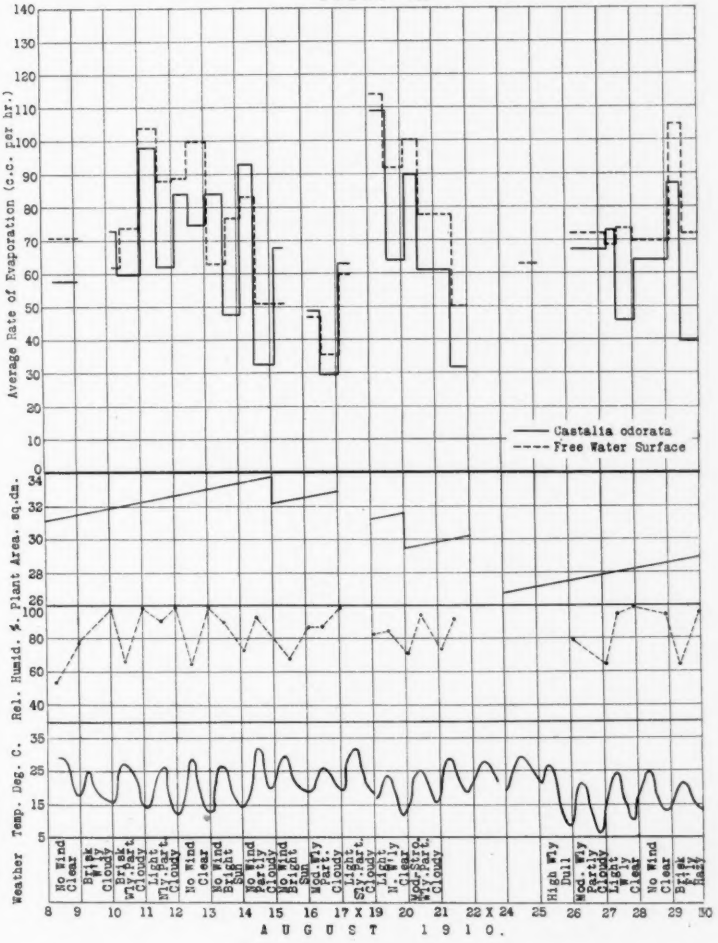
(*d*) *Comparative evaporation from a plant surface and from a free water surface*

Table VI, referred to above, is interesting from the standpoint of a comparison of equivalent areas of plant surface and the surface of free water. It has been commonly held that the transpiring surface of a land plant is normally unable to evaporate as great a quantity of water as is evaporated from a free water surface of the same area and exposed to the same external conditions. GATES (7), experimenting with potted bog plants, makes the statement that three to five times as much water is evaporated from a free water surface as is evaporated from an equivalent area of leaf surface during a hot summer day. This would seem reasonable in view of the fact that the stomatal openings, being widely scattered and not continuous, even when very numerous, do not even approximate the amount of space above a water surface. It should be remembered in this connection, however, that the tissues of water plants are in general very thin, as is evidenced by their early collapse on removing them from the water, and the epidermis shows little or no cuticularization. It is probable, then, that the amount of cuticular transpiration from water plants is greater than is popularly supposed, and that it may compensate to a greater or lesser extent the insufficiency of stomatal openings. In view of these facts the data of table VI show rather interesting results.

Leaving out the case of the arrow-head for the present, it will be seen that in a majority of the day readings the rate of evaporation from the plant surfaces nearly equals the rate from the free water surface, and in some cases even exceeds this rate. Thus, on August 10, 13, 15, and 17, all of the day rates from the plant surfaces exceeded that from the free water surface; on August 14 and 16 all but one showed a greater rate, pickerel-weed in both instances being deficient; but on August 11 there was only one, and on August 12 there were no plant surfaces with a rate greater than that from free water. The transpiration rates at night from the plant surfaces are low compared with those from the free water surface. The one exception is the water lily, whose transpiration rate at night was relatively high compared with that of the other plants, although in no case recorded did it equal that from the

free water surface. Just what is the cause of these variations is not clear, since a survey of the weather conditions for these days gives

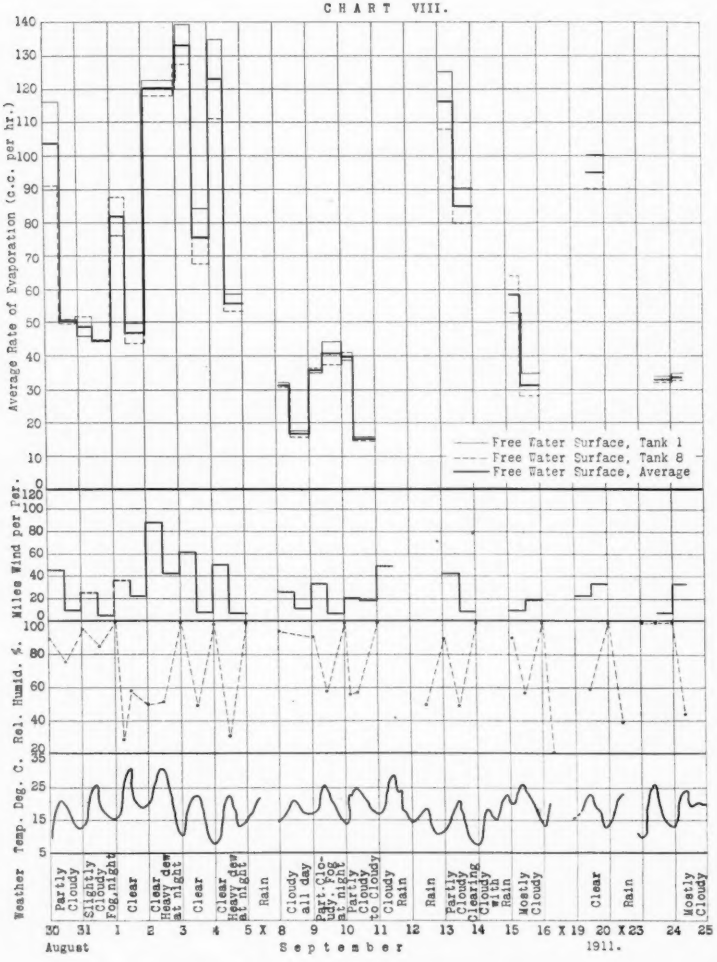
CHART VII.



no indication of the controlling factors. The fact, however, that the majority of the day rates is greater than that from free water, while all of the night rates are less, leads to the supposition that

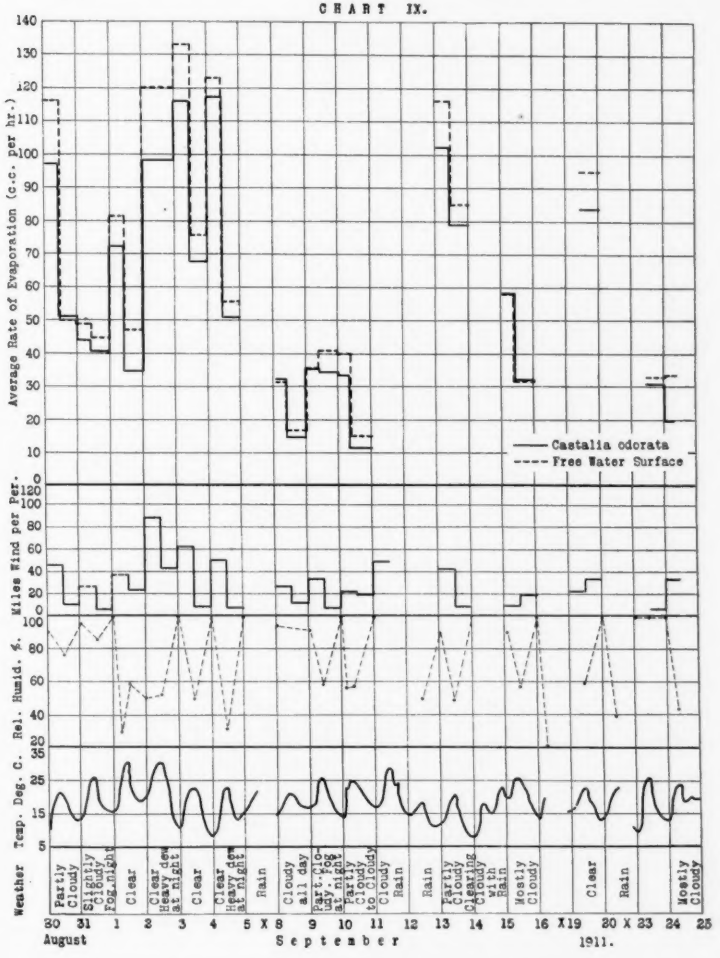
the factor, or combination of factors, responsible for the difference acts differently or with different intensities at night than during the day.

CHART VIII.



Among the plants used the water lily offers perhaps the fairest comparison, since the floating leaves are but slightly elevated above the water surface and physical conditions are thus nearly equal for

leaf and water surfaces. It is said (8) that the purple coloring matter of the lower side of the lily leaves absorbs the sun's rays and in this way tends to increase the internal temperature of the leaves



and hence the transpiration. Experimental evidence seems to be lacking on this point, and it is the belief of the writer that, assuming any slight changes in temperature to be probable, they would be

counteracted or even destroyed by convection currents in the water surrounding the leaf. It is not thought, then, that the increase in transpiration in the water lily is due to temperature differences, but to other causes. The arrow-head is a transition plant, growing, with some modifications, on land, as well as in water, and it is interesting to note that this plant, even when growing in a hydrophytic habitat, behaves more like a typical land plant in the matter of its transpiration.

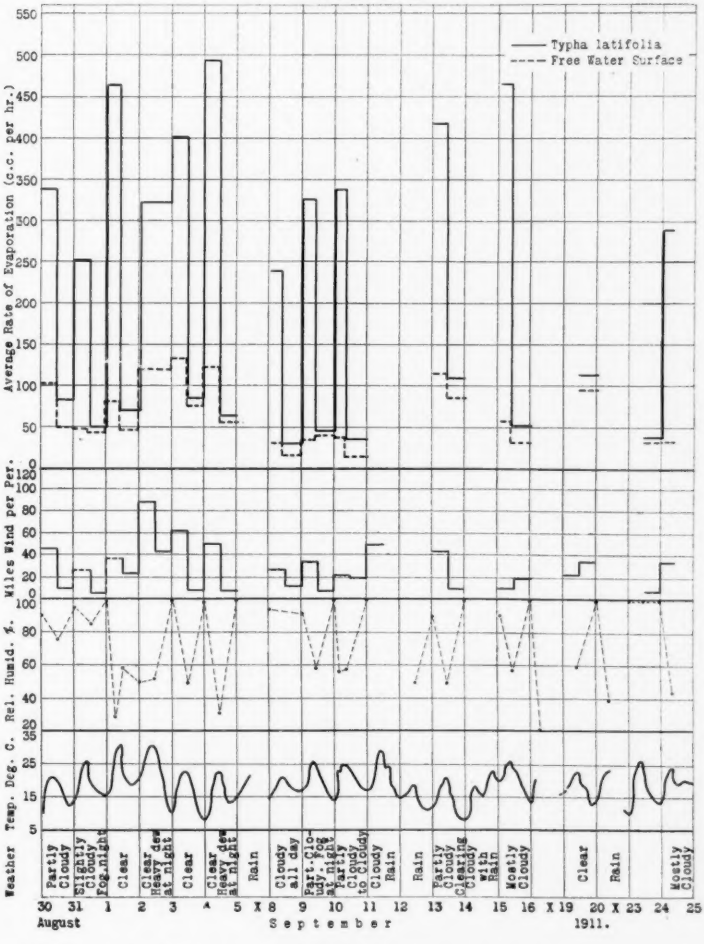
(*e*) *Relation of certain physical factors to transpiration*

An inquiry into the various external factors which exert an influence on transpiration leads to some interesting conclusions. It is not our purpose to consider all of the possible factors which may or may not affect transpiration, nor to consider every factor separately, but rather to consider the combined effect of the more important factors as they occur under natural conditions in the field. Relative humidity, temperature, and wind are quite generally recognized as the principal factors affecting evaporation from an open water surface. In so far as plant transpiration is largely a physical process, omitting, therefore, the phenomena of root pressure, increased protoplasmic activity, and other purely physiological mechanisms, it would be expected that these three factors would be of principal importance in plant transpiration.

1. TEMPERATURE.—The graphs of transpiration shown in charts VIII–XIV show the effect of temperature on the rate of transpiration. With few exceptions the temperature during the night was much less than that during the day. The transpiration graphs show this same relationship as between night and day, the rate during the day being high and correspondingly low during the night. That temperature is not the only factor is shown by the fact that the highest rate of transpiration recorded for most of the plants occurred during the day of September 4, at which time the day temperature was somewhat low. Likewise, during the periods of highest day temperature, that is, September 1, 2, and 15, the transpiration was only moderate. Moreover, on the nights of August 31 and September 3 and 4 the wind velocity was very nearly constant, from 3–5 miles for the period, and the percentage

of relative humidity was about the same. The temperatures on the nights of August 31 and September 4 were nearly equal, and for most of the plants the rates of evaporation were correspondingly

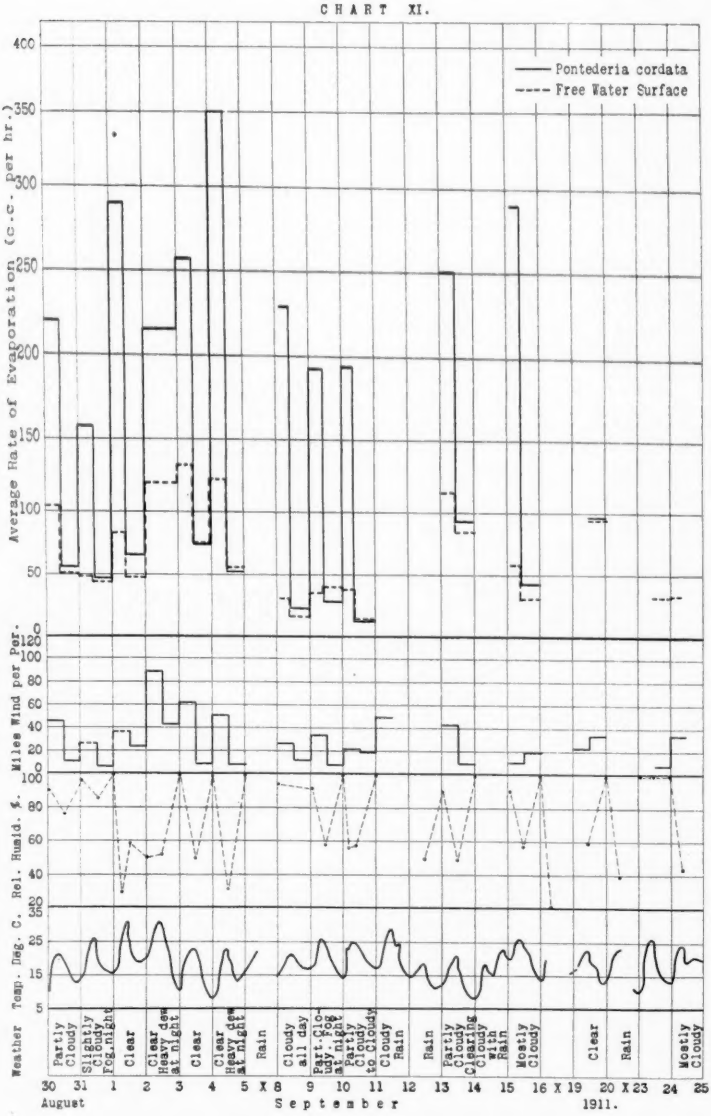
CHART X.



similar. On the night of September 3, however, the temperature was much lower than in the other two cases, but the rate of evaporation was higher.

2. RELATIVE HUMIDITY.—The records of relative humidity are more or less incomplete, owing to the lack of readings during the

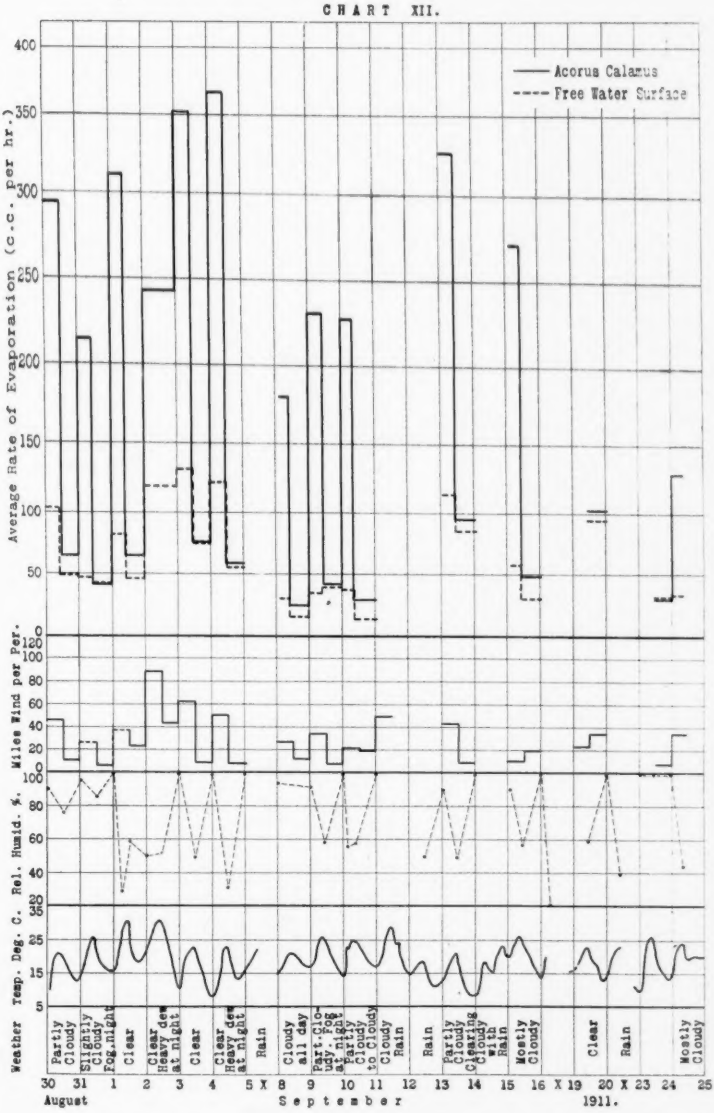
CHART XI.



day; and it is probable that the day humidity was often less than indicated, although it is thought that these readings are relative. However, it was generally true that the humidity was very high

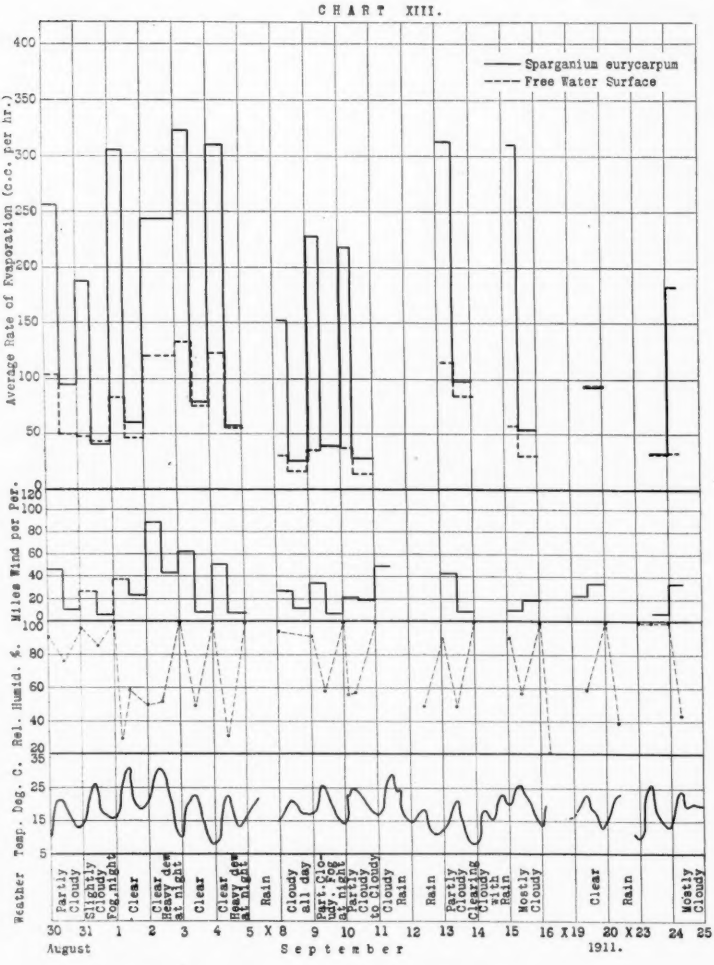
during the night, almost reaching the point of saturation in several instances. Probably this extreme limit was reached in most cases

CHART XII.



between 4 and 6 o'clock in the morning, when the temperature was at its lowest point. Referring again to charts VIII–XIV, it will be observed that periods of high humidity are accompanied by a low

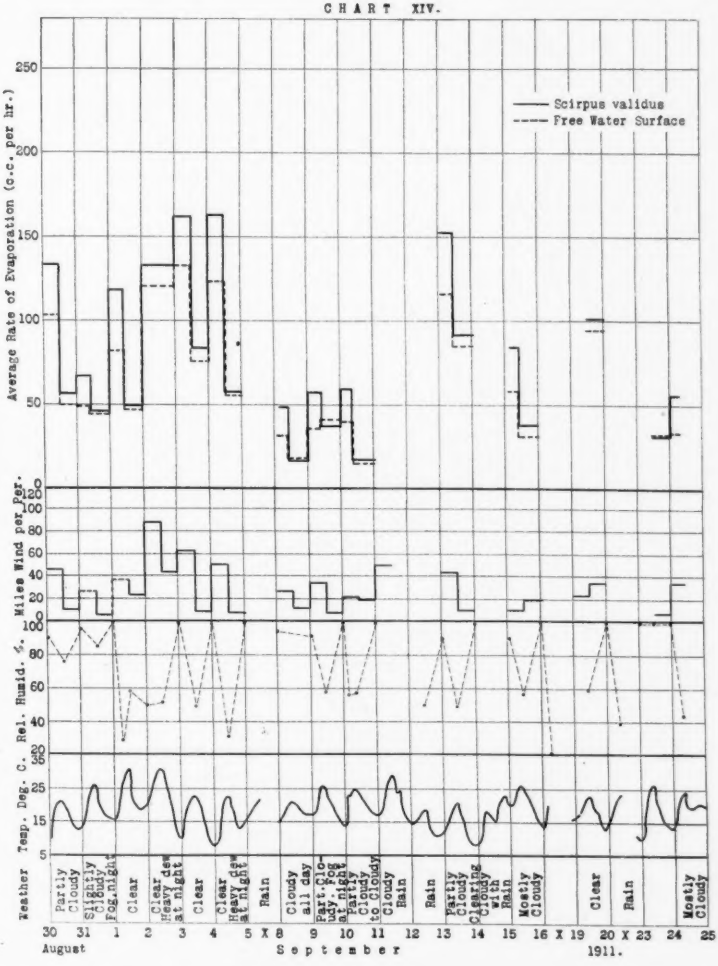
transpiration rate. Also interesting are the results for September 10, when the wind velocity was practically uniform for day and



night, and temperature varied through a small range; transpiration was high while humidity was low, with a reversal of positions when the humidity became high.

3. WIND is undoubtedly an important factor in plant transpiration, at least up to a certain point, that is, to a point at which the

CHART XIV.



wind is strong enough to carry away the moisture as fast as it forms on the surfaces of the plants. It is doubtful, however, if transpiration is materially increased with winds in excess of this amount.

The effect of wind was shown clearly on September 8 (charts VIII–XIV), where relative humidity and temperature did not vary much, but the miles of wind were greater during the day than during the night; the rate of transpiration was greater during the period of greater wind. That wind is a minor factor is shown by the fact that the periods of highest wind velocity are not in all cases periods of highest transpiration rates.

Whether transpiration from plant surfaces is due to one factor more than to another, we are not prepared to say from an examination of the data at hand. Indeed, considering the intimate relation existing between temperature and humidity, it would be impossible to determine the exact influence of the one without being able to maintain the other constant, a state of rare occurrence in nature. And, after all, we are not greatly concerned with these various factors individually, since not one of them of itself is capable of exerting its greatest influence without the accompanying influence of the others. Whether the factors which influence plant transpiration are identical with those which influence evaporation from water surfaces, it is clearly brought out in these experiments that the effects produced on the one and the effects produced on the other are profoundly different in their intensities, and we are led in consequence to the opinion that plant transpiration is not a strictly physical process, but a physiological process as well. The data for 1910 contained in charts I–VII, while not mentioned in detail here, confirm the same conclusions.

Summary

1. Emersed water plants transpire large amounts of water.

2. With one exception (water lily), the evaporation taking place from a water surface occupied by emersed water plants is much greater than that which takes place from a free water surface of the same area and subjected to the same external conditions.

3. The amount of evaporation from a water surface on which water lilies are growing is less than that which takes place from a free water surface of the same area and subjected to the same external conditions.

4. The amount of evaporation from a water surface occupied by emersed water plants depends upon the following factors: (*a*)the species of plant; (*b*) the density of plant stand; (*c*) the amount of plant surface exposed to the evaporating power of the air; (*d*) the height of the plant growth above the level of the water; (*e*) external factors (physical factors, like wind, temperature, relative humidity, etc.); (*f*) internal factors (chemical and physiological phenomena within the plant).

5. Transpiration from emersed water plant surfaces occurs both by day and by night, but transpiration by day is greatly in excess of that by night.

6. For different species there is no constant ratio between rate of transpiration and the area of surface exposed.

7. The rate of evaporation from the transpiring surface of an emersed water plant during the day may equal, and in some cases may exceed, that from a free water surface of the same area; but at night the evaporation from a free water surface is usually greatly in excess of that from a transpiring plant surface.

8. Wind, temperature, and relative humidity undoubtedly have a great influence on the rate of transpiration of emersed water plants, but these factors alone do not explain the great difference existing between transpiration of emersed water plants and the evaporation from a free water surface.

9. These data are of economic importance in indicating what plants should be grown in and what plants should be excluded from storage reservoirs in regions of small rainfall and scant water supply.

In conclusion I desire to extend my hearty thanks to Professor F. C. NEWCOMBE, who has directed this work throughout and who has been a constant inspiration and help, and to Mr. GARDNER S. WILLIAMS and the Eastern Michigan Edison Company for their aid in furnishing the tanks and pontoons and for their suggestions on methods of construction.

UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

LITERATURE CITED

1. BESSEY, C. E., and WOODS, A. F., Transpiration, or the loss of water from plants. Proc. Amer. Assoc. Adv. Sci. **40**:305. 1891. (Abstract.)
2. BURGERSTEIN, A., Die Transpiration der Pflanzen. Jena. 1904.
3. CLAPP, GRACE L., A quantitative study of transpiration. BOT. GAZ. **45**:254. 1908.
4. CLEMENTS, F. E., Research methods in ecology. 1905.
5. EWART, A. J., and REES, BERTHA, Transpiration and the ascent of water in trees under Australian conditions. Ann. Botany **24**:85. 1910.
6. FANNING, T. J., A practical treatise on water-supply engineering. New York. 1877.
7. GATES, F. C., Winter as a factor in the xerophily of certain evergreen ericads. BOT. GAZ. **57**:445. 1914.
8. KERNER VON MARILAUN, A., Pflanzenleben. I. Leipzig und Wien. 1896.
9. MARVIN, C. F., Methods and apparatus for the study of evaporation. II. Instruments. Monthly Weath. Rev. **37**:182. 1909.
10. SCHNEIDER, A., Influence of anaesthetics on plant transpiration. BOT. GAZ. **18**:57. 1893.
11. VESQUE, JULIEN, De l'influence de la température du sol sur l'absorption de l'eau par les racines. Ann. Sci. Nat. Bot. VI. **6**:169. 1878.
12. WOODS, A. F., Some recent investigations on the evaporation of water from plants. BOT. GAZ. **18**:304. 1893.
13. WOODWARD, JOHN, Thoughts and experiments on vegetation. Phil. Trans. Roy. Soc. **21**:193. 1699.

CONTRIBUTIONS TO THE KNOWLEDGE OF THE DIAPHRAGMS OF WATER PLANTS

I. SCIRPUS VALIDUS

LAETITIA M. SNOW

(WITH SIXTEEN FIGURES)

I. Introduction

The form and structure of water plants have been studied by botanists for many years and much has been written on the subject. Many of these investigators, however, have not mentioned the presence or absence of diaphragms in the plants which they have studied, and the reports of those who have considered these structures are often contradictory. The aim of the present paper is to organize these numerous and conflicting reports and to present certain results, which have been obtained chiefly from a study of *Scirpus validus* Vahl. The other forms which have been studied will be referred to as occasion demands. The work has been carried on at Wellesley College and Wood's Hole.

II. Definition of the term "diaphragm"

LEITGEB (**18**) evidently considers a diaphragm as any partition which breaks the continuity of the air passage, for he speaks of them as being present at the nodes of *Hippuris*. DUVAL-JOUVE (**7**), DEBARY (**6**), and SCHENCK (**29**) deny the presence of diaphragms in *Hippuris*, but GOEBEL (**13**) uses this form as an example of a water plant with diaphragms. MEYEN (**20**) states that the hollow stems of the umbellifers and grasses have no cross-walls, but are interrupted at the nodes by masses of tissue. COURCHET (**4**), however, considers that diaphragms are present at the nodes of the umbellifers, and HACKEL (**11***c*) mentions diaphragms of thick tissue at the nodes of grasses. MEYEN (**20, 21**) states that the canals in the leaves of *Ceratophyllum* and in the stem of *Myriophyllum spicatum* end blindly in thick tissue. According to DUVAL-JOUVE (**7**) no diaphragms are found in *Myriophyllum verticillatum*,

but they are present in the leaves of *Ceratophyllum;* while DEBARY (6) denies their presence in both genera.

It is evident, therefore, that some writers consider as diaphragms the thick masses of parenchyma at the nodes of certain plants, while others do not. The loose use of the word has led to much confusion, and it is necessary to define the term. The word "diaphragm" should be reserved for the perforated structures, one to several layers thick, which cross at intervals the air passages of plants. This definition excludes from consideration the woody partitions occurring in the pith of certain trees (*Juglans*, etc.), because they are not only relatively massive, but have been proved by WIESNER and MOLISCH (36) to be impervious to air. Owing to the uncertainty as to the exact meaning of the term, unless perforated diaphragms are distinctly mentioned, one can never be sure that such structures are present in the plant under consideration. In the discussion of the distribution of diaphragms among plants, no effort has been made to distinguish the reports of "perforated diaphragms" from those of "partitions," because many references to diaphragms are without descriptions or figures.

III. Occurrence of diaphragms

A. DISTRIBUTION IN THE VARIOUS PLANT GROUPS

From a study of the outline given under the heading above (see p. 514), it is evident that among the angiosperms the great majority of families in which diaphragms have been found are monocotyledons. It cannot be said, however, that they are restricted to this class, or that they are characteristic of certain genera. I have examined representatives of various families of dicotyledons with the result that diaphragms were found in one species only, *Myriophyllum tenellum*. In this species beautiful perforated diaphragms are present at the nodes, while a second species, *Myriophyllum humile*, and a specimen believed to be another species of the same genus show masses of tissue at these points. Further investigations along this line are in progress.

B. IN PLANT PARTS

Diaphragms have been reported for all parts of plants except flowers and fruits, and in the following order as to abundance:

leaves (especially the blade), upright stems, flower stalks, roots, and rhizomes. Only three instances of the presence of perforated diaphragms in roots have been reported: *Enhalus acoroides* (CUNNINGTON **5**), *Hydrocharis morsus-ranae* (SAUVAGEAU **23**), and *Limnobium Boscii* (MONTESANTO **22**). It is possible, however, that the partitions noted in the roots of *Eriocaulon* and a few species of *Paepalanthus* by HACKEL (**11***c*) may prove to be true diaphragms. Only one reference (DUVAL-JOUVE **7**) has been made to the presence of diaphragms in rhizomes.

C. UNDER VARYING CONDITIONS OF SOIL MOISTURE

LEITGEB (**18**) states that diaphragms are found "especially in leaves of swamp and water plants." DUVAL-JOUVE (**10**), in his study of partly submerged grasses, found air spaces and diaphragms present in the immersed parts only. SOLEREDER (**32**), on the other hand, reports their presence in the aerial as well as the submerged parts of the leaves of *Stratiotes*. DUVAL-JOUVE (**9**) found no diaphragms in the leaves of *Iris germanica* growing in a dry habitat, but found them in *I. pseudacorus* and *I. foetidissima* growing in water or wet places. He did not, however, test the same species in the two habitats.

My work upon *Scirpus validus* has shown no apparent difference, as to the presence or structure of diaphragms, between the immersed and the aerial parts. Experiments are at present in progress to test the possibility of growing this species in drained soil, and to investigate any structural changes which may take place under drier conditions.

IV. Structure

A. OF DIAPHRAGMS

In accordance with the reports for various plants, the diaphragms of *Scirpus validus* are one to several layers thick. Commonly in old stems the greater extent of the diaphragm is composed of one layer of cells, which increases to several layers around the cross-bundle (fig. 7). As a rule, a diaphragm extends over one air space, but DUVAL-JOUVE (**9**) states that those of *Cyperus Papyrus*, *Thalia dealbata*, *Butomus umbellatus*, and *Sagittaria*

lancifolia may extend over several spaces; and SCHWENDENER (30) finds the same to be true for *Papyrus antiquorum*. Only in rare instances do the diaphragms of *S. validus* extend over more than one space.

The shape of the cells varies, with the species studied, from polygonal cells with tiny air spaces at the corners, to stellate cells with very much elongated arms. A study of *S. validus*, taken in connection with the reports of DUVAL-JOUVE (9) for *S. lacustris*, *S. littoralis*, and *S. triquetrii*, and of DEBARY (6) and MEYEN (21) for *S. lacustris*, suggests "scirpus type" as an appropriate term by which to designate diaphragms showing the peculiar arrangement of cells characteristic of these species. In this type the cells are elongated and have very short arms. These long narrow cells occur

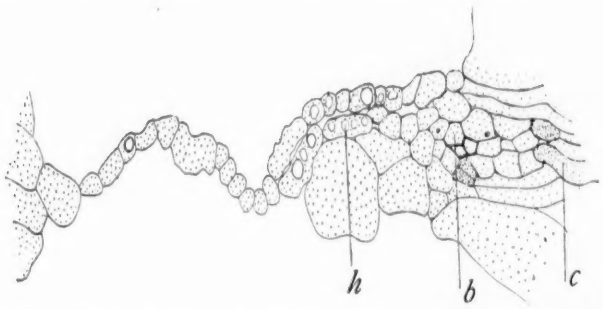


FIG. 1.—Flax seedling: longitudinal section through hypocotyl: *c*, ordinary cortical cells; cells are elongating in the direction of food current passing to meristem beyond *h*; *b*, young bundle; ×110.

in groups of two, three, four, or five, the usual number being four. While the cells in a single group are all elongated in the same direction, the different groups (with certain exceptions to be noted later) have their axes of elongation pointing in different directions. DUVAL-JOUVE (9) states that *Sagittaria lancifolia* has this type of diaphragm, except that the cells are in groups of two (his figure, however, does not agree with the statement), and that *S. sagittifolia* and *Alisma Plantago* resemble *S. lancifolia*. In another paper (10) he states that the diaphragms in "certain species of grasses" have cells in groups of four. A study (as yet incomplete) of the different species of *Scirpus* leads to the conclusion that some species of the genus may possess more than one type of diaphragm. It has not yet been determined whether any correlation

exists between the different types of diaphragm and the presence or absence of cross-bundles.

Although both vascular and non-vascular diaphragms are mentioned by writers, the former so far outnumber the latter that some authorities consider the chief function of diaphragms to be the support of the cross-bundles. In *Scirpus validus* the presence of cross-bundles is so nearly universal that the relatively few instances where they cannot be found lead one to suspect that in these cases the material has been broken or a section or two lost at the critical point.

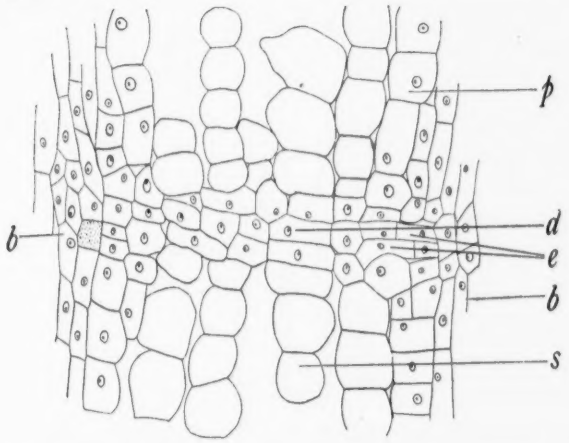


FIG. 2.—*Scirpus validus:* longitudinal section of very young stem: diaphragm cells elongating to form cross-bundle; nuclei indicate the greater density of protoplasmic contents of cells of diaphragm and partition walls of spaces; some nuclei were not demonstrable but were placed arbitrarily; *p*, partition cells; *d*, diaphragm cells; *b*, young longitudinal bundle; *s*, cells of space; *e*, elongating cells; ×175.

B. OF CROSS-BUNDLES

DUVAL-JOUVE (**9**) describes the cross-bundles of *Musa paradisiaca* as containing large spiral vessels; those of *Butomus umbellatus*, *Alisma Plantago*, *Sagittaria lancifolia*, and *S. sagittifolia* as bundles of tracheae. He states in one report (**8**) that the cross-bundles connect with the outer part of the longitudinal bundles. In his next paper (**9**) he describes a cross-bundle as articulating itself with the side of the longitudinal bundle, a little back of the large vessels and opposite the interior region of tracheids and small vessels. A figure in a third paper (**10**) shows a cross-bundle uniting with the phloem.

A study of the cross-bundles of *Scirpus validus* leads to the conclusion that both conditions occur, and are dependent upon the age of the diaphragm. In the very young stem the cells of the cross-bundle are similar to those of the diaphragm and connect with the phloem (figs. 2 and 12). Later the cells greatly elongate, some of those in the center of the bundle become transformed into tracheids with very indistinct spiral (?) markings, and a secondary connection with the xylem of the longitudinal bundle is established (figs. 3 and 4).

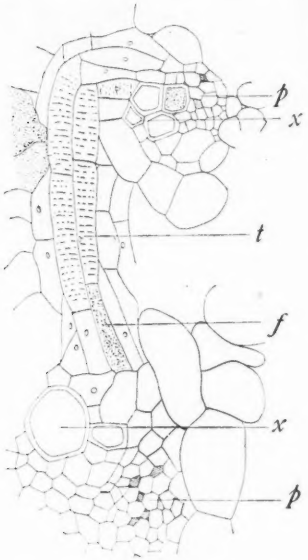


FIG. 3.—*Scirpus validus:* cross-section of stem: two longitudinal bundles connected by a cross-bundle; connection originally with phloem (*p*); tracheids (*t*) have formed and made secondary connection with xylem (*x*); the connection is not yet established with larger bundle; this bundle lies near the edge of a space, but is not connected with a diaphragm; *f*, food storage cells; ×175.

DUVAL-JOUVE (**9**) mentions the fact that in *Sagittaria lancifolia* the bundles do not run on the diaphragms but in them, thus implying that the reverse is usually the case. The diaphragms of *Scirpus validus* run in the diaphragms, as is shown in fig. 5.

V. Origin

A. OF THE STELLATE PARENCHYMA

The canals of many water plants are filled with a network of stellate cells. In the case of *Scirpus validus* the cells on the upper and lower surfaces of the diaphragms connect directly with these stellate cells, and in some places have been seen to grade into them. It is necessary, therefore, to inquire into the origin of the stellate tissue.

SCHACHT (**28**) states that the arms of the stellate cells are caused by greater growth, due to a greater amount of nourishment, at certain points. LEITGEB (**18**) discusses the development of this

tissue at some length, and considers the star-shape to be a result of adhesion at certain points, combined with the growth of the surrounding tissue and the "pressure of the secreted air." That the growth of the surrounding tissue causes a pulling out of the cell is indicated by the "diminishing cell body." He adds that the arms, after having been formed, increase in size (presumably by growth). DUVAL-JOUVE (**7**) considers that the body of the cell does not increase in size, but that the arms grow out as rays; the presence of apparently bifurcated rays indicates a pulling out of the body. In another paper (**10**) he speaks of the pulling out of the cells from the points of contact. SCHWENDENER (**30**) believes stellate cells to be due, not directly to a pull, but to growth under a tension caused by the faster growth of the surrounding tissue. DEBARY (**6**) speaks of cells growing into long arms. LE BLANC (**17**) gives the same explanation as LEITGEB (whose paper he has apparently not seen), and proves the existence of tension in stellate tissue by an experiment. By bursting one of the stellate cells in a diaphragm, he found that a round hole resulted, which was larger than the original cell, and which was caused by a retraction of the surrounding cells.

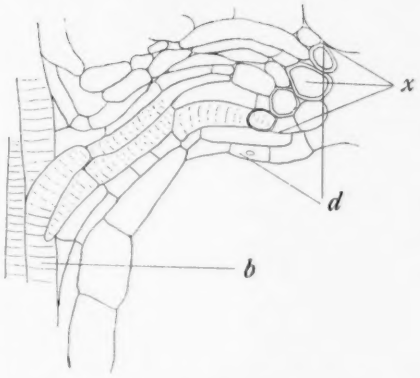


FIG. 4.—*Scirpus validus:* longitudinal section of stem: cross-bundle curving, part in cross-section (*x*) and part in longitudinal section; xylem making connection with xylem of longitudinal bundle (*b*); ×175.

LEITGEB (**18**) does not explain the formation of the intercellular spaces otherwise than by the pressure of the secreted air. TSCHIRCH (**34**) thinks that intercellular spaces are formed by a splitting of the primary membrane, because the spaces are covered with a substance giving the same reaction as the primary membrane. GOEBEL

(13), in his study of aerenchyma, came to the conclusion that the cells adhere by the thickenings of the walls, while the pits remain free. MANGIN (19) believes the split to be due to a gelatinization of pectates in the wall, which substances, in consequence, line the intercellular space thus formed.

A study of the stellate parenchyma of *Juncus effusus* leads me to the conclusion that SCHWENDENER has given the correct explanation of the origin of this type of cells. All cells pass through a curve of growth. The center is the oldest part of the pith and reaches the mode of the curve first. As the growth in this region becomes slower, the outer parts are approaching the mode of the curve.

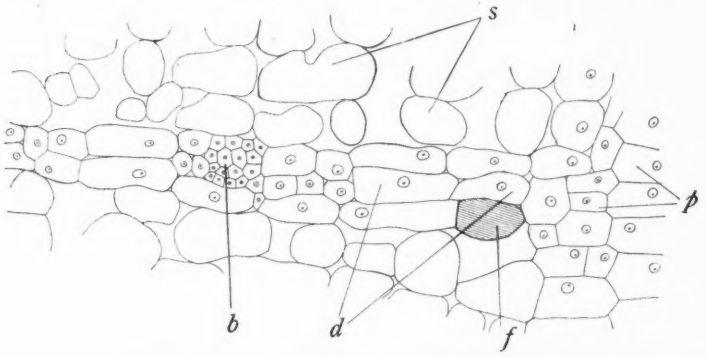


FIG. 5.—*Scirpus validus:* longitudinal section of young stem: diaphragm with cross-section of cross-bundle; nuclei as in fig. 2; *s*, cells of space; *p*, partition cells; *b*, cross-bundle; *d*, ordinary diaphragm cells; *f*, food storage cells; ×175.

Thus the growth of the central cells cannot keep pace with the growth of the outer cells and they are, in consequence, pulled out into arms. The slower the growth the greater the proportion of pull, and consequently very old cells have quite long, slender arms. By taking an average of the longest and the shortest diameters of the bodies of many pith cells at the same stage of development, and comparing it with similar averages for pith cells at different stages, it was found that the cell body passed from 25.6 μ at the tip of the stem, to 21.5 μ a little farther back, and to 17.1 μ still farther back. In any one section the cells at the center are at a much later stage of development than those toward the outside of the stem (fig. 16).

B. OF DIAPHRAGMS

LEITGEB (**18**) states that he cannot account for the fact that some cells do not pull out, but remain as diaphragms. MEYEN (**21**), studying *Scirpus lacustris*, and FALKENBERG (**12**), studying *Typha* leaves, state that diaphragms result from stellate parenchyma by a separation of this tissue into layers. CUNNINGTON (**5**) finds that the diaphragms in the leaves of *Enhalus acoroides* arise from small cells cut off from the original mesophyll cells. These small cells increase in one plane and form plates separating the other mesophyll cells, which elongate in a plane perpendicular to these plates and thus separate them by spaces.

In *Scirpus validus* there are no special cells which give rise to diaphragms. In *Juncus effusus* the parenchyma splits into layers which retain an occasional vertical connection (fig. 15). In longitudinal sections of *Scirpus* a similar layering may be observed. The cells of some of the layers retain their meristematic character and continue to divide and to keep pace with the growth of the surrounding tissues, thus forming diaphragms. The other cells become stellate by the process already described (figs. 2, 5, 12, 13).

C. OF THE GROUPS OF CELLS IN THE DIAPHRAGMS

Several writers have noted or figured the diaphragm cells in groups of four. DUVAL-JOUVE (**9**) reports this arrangement for several species of plants, but offers no explanation as to the origin of the groups. DEBARY (**6**) believes each group of cells in the diaphragms of *Scirpus lacustris* to originate from one mother cell.

From a comparison of figs. 12 and 13, it seems evident that such an origin as that suggested by DEBARY is reasonably probable. The number, however, is not invariably four, but groups of three and five also appear (fig. 6). The reason for the formation of two, three, or four walls parallel to the long axis of the cell is not easily explained in terms of cytological mechanics. It was suggested to me that a study of the adventitious buds of flax seedlings might throw light upon the subject. Flax seedlings were grown, therefore, until the cotyledons had opened, and were then decapitated. After about

a week or ten days small swellings (adventitious buds) appeared on the hypocotyl. It is found, upon studying longitudinal sections of these hypocotyls, that the meristem of the bud is composed of small cubical cells which have arisen, by division, from the epidermis and outer cortical cells. Deeper cortical cells, however, are found to be elongating and apparently dividing parallel to their long axes, that is, in the direction of the current of food materials passing to the growing meristem (fig. 1).

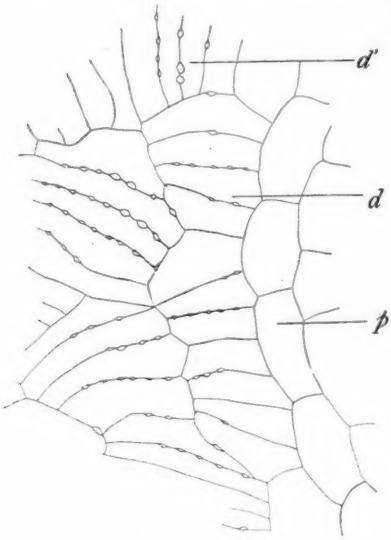


FIG. 6.—*Scirpus validus:* cross-section of older stem: *p*, partition cells; *d*, diaphragm cells perpendicular to the partition; *d'*, cells not in position characteristic of cells adjoining partitions; ×175.

It is well known that HABERLANDT (**15**) correlates the shape of the palisade cells with the transportation of the products of photosynthesis. A similar elongation of cells for the purpose of conduction is found in the secondary transfusion tissue of *Cycas*, where, according to WORSDELL (**38**), the ordinary mesophyll cells become modified in order to supply water to the parts of the leaf which are distant from the bundle. From GOEBEL'S study of adventitious buds (**14**) it is seen that the bundle becomes differentiated first in the leaf and afterward extends itself backward, until it reaches and becomes connected with a bundle in the stem. This elongation of cells to continue the bundle may be interpreted as a result of the current of food materials passing to and from the growing leaf. In a similar way the current of food materials from the cross-bundle to the partition walls of the air space may determine the direction of the walls of the groups of cells in the diaphragms.

VI. Function of diaphragms

A. MECHANICAL

1. *To resist strain.*—SCHWENDENER (**30**) considers diaphragms to be girders; HABERLANDT (**15**) and LE BLANC (**17**) agree with him, but believe strengthening to be only one of their functions. This is probably true. If certain species of *Juncus* with nodose stems and leaves be compared, it will be seen that those forms having firm, stiff outer walls have a smaller number of cross-partitions than have those with softer walls.

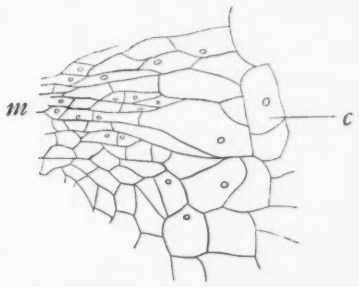


FIG. 7.—*Scirpus validus:* longitudinal section of stem: diaphragm varying in thickness; cross-bundle (*m*) at edge of diaphragm establishing connection with a longitudinal bundle beyond section; cells stippled to distinguish from spaces; *c*, cut arms of cells; ×110.

2. *Support of cross-bundles.*—LEITGEB (**18**), DUVAL-JOUVE (**9**), DEBARY (**6**), and SAUVAGEAU (**25**) definitely state that diaphragms are for the support of cross-bundles. LE BLANC (**17**) assigns it as one of their functions. Where cross-bundles occur there can be no doubt as to the value of such support. It cannot be assigned as a function of all diaphragms, however, because non-vascular diaphragms appear to be characteristic of certain plants.

B. TO PREVENT THE ENTRANCE OF WATER

GOEBEL (**13**) believes that diaphragms are of use in keeping water from entering broken parts, stating that it takes great pressure to infiltrate the air passages. It is quite probable that the small size of the perforations in the diaphragms prevents the entrance of water against the pressure of the contained air. The fact that, in order to force killing fluids into the tissues of plants with diaphragms or with small intercellular spaces, it is necessary to exhaust the air with a pump indicates the difficulty with which water penetrates small openings against air pressure. This

difficulty might be increased by the presence of cutin on the walls of the diaphragm cells, but the walls of these cells in *Scirpus validus* give the cellulose reaction only.

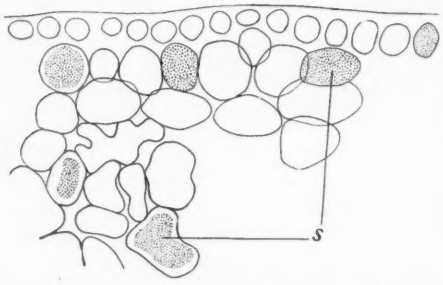


FIG. 8.—*Scirpus validus:* a few cells from cross-section of leaf of young bud: epidermis, parenchyma, and spongy tissue of air space shown; section treated with Fehling's solution; strong reaction indicated by stippling (*s*); merely size, position, and shape of cells indicated; ×175.

SAUVAGEAU (**27**) found that after injecting the stem with water, some of the canals were suberized, and concluded that suberization takes place after contact with water, to prevent infiltration of the surrounding tissues. As he offers no direct proof of suberization following contact with water, definite conclusions cannot be derived from this work.

C. TO AID IN CIRCULATION OF AIR

HABERLANDT (**15**) and LE BLANC (**17**) include this among the functions of diaphragms. It seems evident that, given partitions, it is advantageous to have them perforated, to allow circulation of air. The statement made by GOEBEL (**13**) that nonperforated diaphragms in *Pontederia crassipes* (*Eichhornia*) allow circulation of air needs proof.

D. NUTRITION

LE BLANC (**17**) supports CHATIN[1] in believing nutrition to be one of

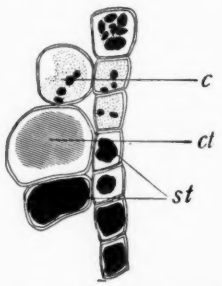


FIG. 9.—*Scirpus validus:* a few cells from cross-section of leaf of young bud: treated with Fehling's solution, I in KI, and $K_2Cr_2O_7$; *c*, cell showing cytoplasm and scattered starch grains; *ct*, cell with contents plasmolyzed, starch grains not distinguishable; *st*, cell which has reduced Fehling's solution and given tannin test with $K_2Cr_2O_7$; ×175.

[1] CHATIN, ADOLPHE, Anatomie comparée des végéteaux. Paris. 1856–1862. I have not been able to obtain this publication.

the functions of diaphragms. Food manufacture undoubtedly takes place, to some extent, in very young diaphragms of *Scirpus validus* which are close to the exterior. As the stem grows larger and the diaphragms are removed from the exterior by the growth of the outer tissues, they lose their chlorophyll and appear glistening white.

E. STORAGE

That food (or waste) is stored in diaphragm cells is evident at a glance (figs. 12 and 13), but the nature of the stored material has not been definitely determined. SAUVAGEAU (**24–27**) notes secretory cells in various forms of water plants, and in certain places

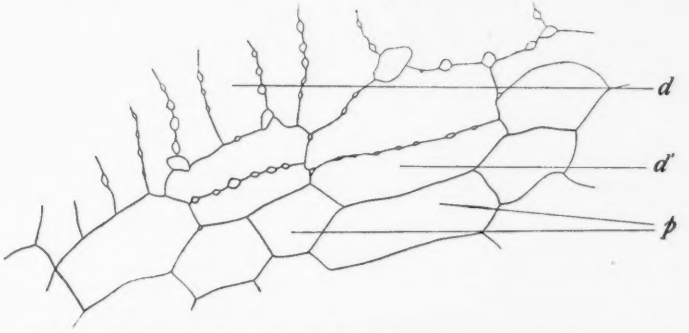


FIG. 10.—*Scirpus validus:* cross-section of stem at edge of diaphragm: *d*, diaphragm cells in position characteristic for cells adjoining a partition; *d'*, cells of partition which have assumed the character of diaphragm cells and are therefore not in the characteristic position; *p*, partition cells; ×175.

definitely calls the contents tannin. SOLEREDER (**31**) records the presence of tannin-bearing cells in the diaphragms and the walls of air spaces of the Hydrocharitaceae. He tested with vanillin and concentrated hydrochloric acid, as suggested by HARTWICH and WINCKEL (**16**), and obtained the phloroglucin reaction. He obtained the same result with HCl alone, which showed that an aldehyde, similar in action to vanillin, was present. He found in *Vallisneria* that the contents of certain cells gave the tannin reaction with iron, while other cells were filled with a clear oil-like material.

In material of *Scirpus validus* killed with chromacetic acid, many brown storage cells appear. An investigation of the chemical

nature of the storage material led to the following results. Fresh sections after having been boiled in Fehling's solution showed many red-brown cells (fig. 8). The sections were then washed in water and treated with a solution of iodine in potassium iodide. These "sugar cells" remained red-brown, while the others gave a strong starch reaction. The sections were again washed in water and then treated with potassium bichromate, and the reddish cells turned very dark brown. Fig. 9 shows a portion of a section at this stage. Tested with ferric chloride these "sugar cells" gave the characteristic tannin reaction. TRIMBLE (33) states that glucose is frequently present with tannin, and also that tannin will reduce Fehling's solution; consequently the reactions described above may be due to tannin and glucose or to tannin alone. TRIMBLE also found that in the rhizome of *Acorus Calamus*, the tannin-bearing cells were quite distinct from the starch-bearing cells.

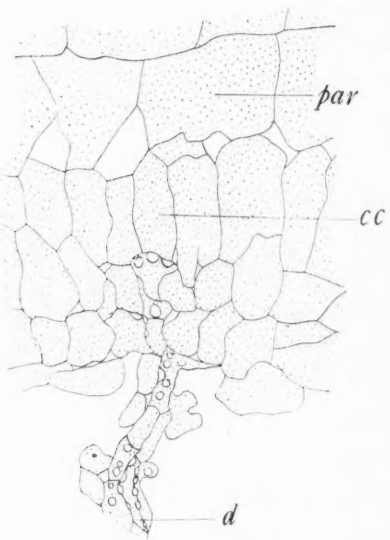


FIG. 11.—*Scirpus validus:* longitudinal section of stem: *d*, diaphragm extending into partition; *par*, ordinary, polygonal, partition cells; *cc*, partition cells elongated for conductive function; circles in cells indicate cut arms; stippling to distinguish cells from spaces; ×110.

When fresh specimens of *Scirpus validus* were tested with vanillin and concentrated HCl, according to the method described by HARTWICH and WINCKEL (16), it was found that numerous cells turned ruby red. This reaction showed the presence of phloroglucin or some related tannoid. The reaction did not take place with HCl alone, therefore the necessary aldehyde was not present in the cells. Washing the sections in water caused the red color to disappear, and subsequent treatment with $K_2Cr_2O_7$ brought out strongly the tannin reaction. This took place at once, instead of slowly, as before the phloroglucin test.

To ascertain if gallic acid was present, fresh sections were treated with potassium cyanide (TRIMBLE 33). The majority of the sections gave no reaction, but one or two showed a faint diffuse pinkish tint at one corner where there was a mass of very dark brown sclerenchyma cells. Left over night, many cells turned a very pale brown, thus showing the presence of tannin rather than gallic acid. When the sections, which had been washed after

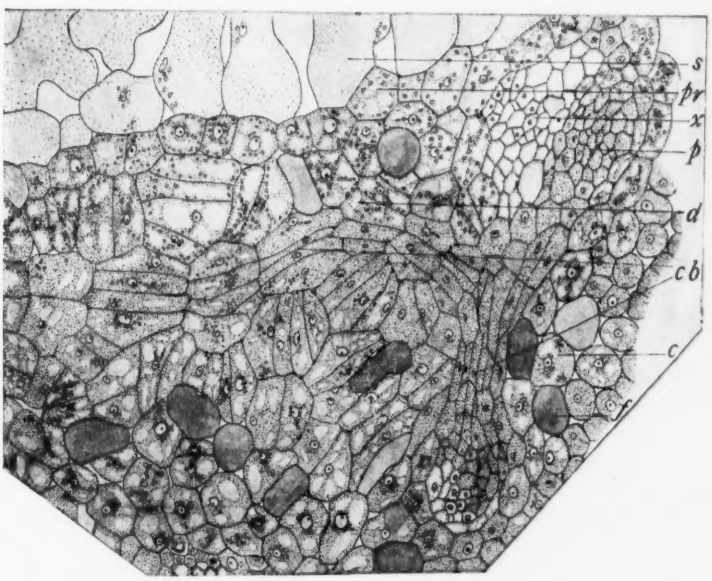


FIG. 12.—*Scirpus validus:* cross-section of tip of very young stem: two longitudinal bundles and connecting cross-bundles (*cb*); the latter runs in a diaphragm (*d*); cross-bundles connect with phloem (*p*); diaphragm cells starting to form groups; note similarity between cells of diaphragm and of cross-bundles; *c*, cortical parenchyma; *pr*, partition wall separating two spaces; *s*, cells of space; *x*, xylem; *f*, food storage cells; ×175.

the phloroglucin test, were treated with KCN, many cells (presumably those which had responded to the previous test) immediately turned dark brown. It is thus seen that after the phloroglucin test the tannin reaction takes place with great rapidity and clearness.

Since the fresh cells give the tannin reaction with $K_2Cr_2O_7$ and $FeCl_3$, and also the phloroglucin reaction, it is possible that the food is stored as some tannin compound containing the phloroglucin radical. I am not sufficiently familiar with the chemistry

of the tannin compounds to make any further suggestions as to the nature of the stored material.

Storage cells are very abundant in the diaphragms and in the parenchyma of the stems of *Scirpus validus*, but are also present in

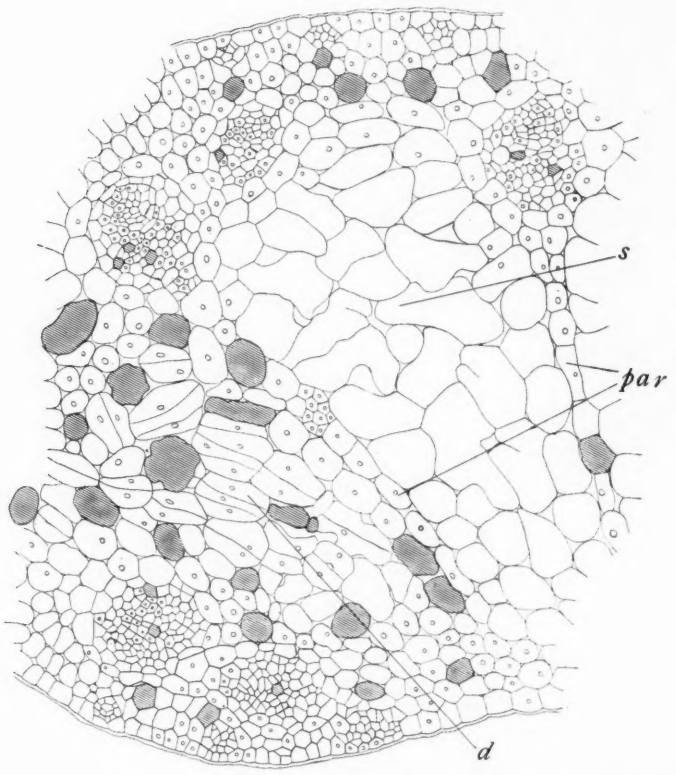


FIG. 13.—*Scirpus validus:* cross-section of tip of very young stem: *par*, partitions separating three spaces; *s*, cells of space which will become stellate; *d*, young diaphragm; note great number of food storage cells in diaphragm; ×110.

the scales of young buds, the spongy parenchyma of the rhizome, and in both longitudinal and cross-bundles. They have not been observed in the young roots of this species.

F. CONDUCTION

To the above-mentioned functions may be added that of conduction. An examination of figs. 6, 10, and 12 will show that the

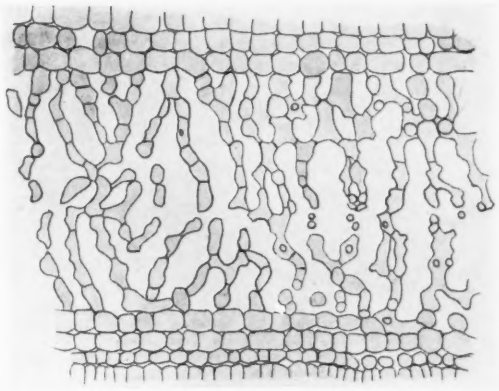


FIG. 14.—*Juncus effusus:* a few cells from cross-section of stem, showing transition from rounded cells on outer edge of pith to stellate cells nearer the center; ×110.

FIG. 15.—*Juncus effusus solutus:* longitudinal section of stem showing formation of cross-layers in stellate parenchyma; ×35.

groups of cells adjoining the cross-bundle and the partition walls of the air spaces have their long axes perpendicular to the bundle and the walls respectively. This is an almost universal condition; where

there are exceptions, some at least can be shown to be partition cells which have secondarily assumed the character of diaphragm cells (fig. 10). Around storage cells the diaphragm cells frequently assume a rosette arrangement (fig. 16), apparently for conductive purposes. The fact that the first connection of the cross-bundle with the longitudinal bundle is with the phloem also lends weight to this suggestion. Longitudinal sections show that the diaphragm cells extend a short distance into the partitions, and that the ordinary polygonal partition cells become elongated and slope toward

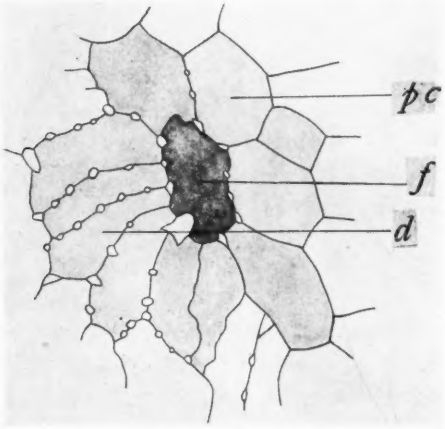


FIG. 16.—*Scirpus validus:* a few cells at edge of diaphragm: *f*, food storage cell; *d*, diaphragm cells leading to or from storage cell; *pc*, cortical parenchyma; ×175.

the diaphragm, thus suggesting a conductive function (fig. 11). From these conditions it seems reasonable to conclude that conduction is one function of the diaphragms of *Scirpus validus*.

Summary

1. Diaphragms, although present in many monocotyledons, are not restricted to that group. The present state of our knowledge, however, does not allow us to make definite statements as to their distribution.

2. Diaphragms are especially characteristic of leaves, but have been reported for all parts of plants except flowers and fruits.

3. Diaphragms have been found in immersed and in aerial parts of plants.

4. Diaphragms appear to be characteristic of plants growing in water or very wet places.

5. The structure of diaphragms varies: (*a*) they may be one to several layers thick; (*b*) the cells vary from polygonal to stellate; in the "scirpus type" the cells are in groups (usually of four) and are long and narrow, with short arms; (*c*) the presence of cross-bundles appears to vary with the form studied. In *Scirpus validus* nearly all the diaphragms have bundles in them.

6. The cross-bundle is made up of xylem and phloem. At first the connection with the longitudinal bundles is with the phloem, but later a secondary connection is made with the xylem.

7. The stellate cells originate from ordinary parenchyma cells by the differential growth of the cells from the inside outward.

8. Diaphragms in *Scirpus validus* arise by a division of the parenchyma into layers, some of which retain their meristematic character, while the remaining cells gradually cease growing and become the slender stellate cells of the air spaces.

9. Each group of four cells of the diaphragm of *Scirpus* spp. arises from a mother cell. The formation of dividing walls parallel to the long axes of the cells is probably determined by the current of food materials passing from the cross-bundle to the partition walls of the space.

10. Diaphragms have the following functions: (*a*) to resist strains and keep the spaces open; (*b*) to support cross-bundles; (*c*) to prevent entrance of water by the small size of the perforation; (*d*) perforations permit air to circulate; (*e*) while young and green, to manufacture carbohydrates; (*f*) to store food: (i) this is possibly in the form of some tannin compound containing the phloroglucin radical, and may or may not be associated with glucose; (ii) this substance is stored in special cells which are distinct from the starch-bearing cells; (*g*) to conduct food materials from the cross-bundle to the partition walls of the space.

My thanks are due Professor KARL M. WIEGAND for his kindly assistance in the identification of the species studied, and

to Professor B. M. DUGGAR for helpful suggestions during that part of the investigation which was conducted at Wood's Hole.

WELLESLEY COLLEGE

THE DISTRIBUTION OF DIAPHRAGMS IN THE VARIOUS GROUPS OF PLANTS

1. PTERIDOPHYTES.—They are reported for ferns and *Equisetum* by LEITGEB (**18**), but are not mentioned by COSTANTIN (**3**) in his report on *Equisetum*.

2. SPERMATOPHYTES.—

a) No mention has been made of the presence of diaphragms in the gymnosperms.

b) Diaphragms have been observed in the following families of angiosperms:

(1) *Dicotyledons:*

In Nymphaeaceae by LEITGEB (**18**), SOLEREDER (**31**), and LE BLANC (**17**). Their presence in *Nelumbium* (*Nelumbo*) is denied by DEBARY (**6**).

In Ceratophyllaceae by DUVAL-JOUVE (**7**), but their presence is denied by MEYEN (**20, 21**), DEBARY (**6**), and SCHENCK (**29**).

In Haloragidaceae by LEITGEB (**18**) and GOEBEL (**13**), but their presence is denied by MEYEN (**20, 21**), DUVAL-JOUVE (**7**), DEBARY (**6**), and SCHENCK (**29**).

In Gentianaceae by DUVAL-JOUVE (**9**), but their presence in *Limnanthemum nymphoides* is denied by DEBARY (**6**).

In Rubiaceae by UNGER (**35**) for *Richardia aethiopica* (authority not noted). In ENGLER and PRANTL *Richardsonia* is given as a synonym for *Richardia*, but the species *aethiopica* does not appear, and it is not safe to conclude from this report that diaphragms occur in this family.

In Umbelliferae by LEITGEB (**18**) and (at nodes) by COURCHET (**4**), but their presence is denied by MEYEN (**20**).

In Compositae by LEITGEB (**18**).

COSTANTIN (**3**) made an extended study of water plants, including many families, the greater number of which were dicotyledons, but he does not mention the presence of diaphragms. LE BLANC (**17**) states that they occur only in monocotyledons and the related Nymphaeaceae.

(2) *Monocotyledons:*

In Typhaceae by LEITGEB (**18**), DUVAL-JOUVE (**7, 9**), and FALKENBERG (**12**).

In Pandanaceae by MEYEN (**20**).

In Sparganiaceae by DUVAL-JOUVE (**7, 9**).

In Potamogetonaceae by DUVAL-JOUVE (**9**), SAUVAGEAU (**25, 26, 27**), and MEYEN (**21**). Their presence is denied in *Zostera* and *Posidonia caulini* by DEBARY (**6**). SAUVAGEAU (**25**) reports them for *Zostera*, but does not consider the thin partitions extending from epidermis to epidermis in the

leaves of *Posidonia caulini* and *Cymodocea antarctica* to be diaphragms. He does not mention diaphragms in his reports on *Phyllospadix* (26) and *Ruppia* (27).

In Najadaceae by LEITGEB (18).

In Hydrocharitaceae by MEYEN (20), SAUVAGEAU (23, 24, 25), SOLEREDER (32), MONTESANTOS (22), and CUNNINGTON (5). BALFOUR (1) states that the canals of *Halophila* end at the nodes in thick tissue, and CASPARY (2) makes the same statement for the Hydrilleae. SAUVAGEAU (24) does not mention diaphragms in his report on *Halophila*.

In Aponogetonaceae by DUVAL-JOUVE (9) and in ENGLER and PRANTL (11*c*).

In Juncaginaceae in ENGLER and PRANTL (11*c*).

In Alismaceae in ENGLER and PRANTL (11*c*), by DUVAL-JOUVE (9), and MEYEN (20).

In Butomaceae in ENGLER and PRANTL (11*c*) and by DUVAL-JOUVE (9). No mention of diaphragms is made by COSTANTIN (3) in his report on *Butomus*.

In Gramineae by LEITGEB (18), DUVAL-JOUVE (7, 8, 9, 10), and MEYEN (20).

In Cyperaceae in ENGLER and PRANTL (11*c*), by MEYEN (20, 21), LEITGEB (18), DUVAL-JOUVE (7, 9), SCHWENDENER (30), FALKENBERG (12), and DE-BARY (6).

In Araceae by MEYEN (21), LEITGEB (18), DUVAL-JOUVE (9), and WEISS (37).

In Eriocaulaceae (?) in ENGLER and PRANTL (11*c*).

In Mayacaceae. The description of the leaves in ENGLER and PRANTL (11*c*) suggests the presence of diaphragms.

In Pontederiaceae in ENGLER and PRANTL (11*c*), by MEYEN (20), DUVAL-JOUVE (7, 9), and GOEBEL (13).

In Juncaceae in ENGLER and PRANTL (11*c*), by DUVAL-JOUVE (7, 8, 9), and SCHWENDENER (30).

In Liliaceae by MEYEN (20) and DUVAL-JOUVE (9).

In Iridaceae by DUVAL-JOUVE (9).

In Musaceae in ENGLER and PRANTL (11*c*), by MEYEN (20), and DUVAL-JOUVE (9).

In Cannaceae by MEYEN (20) and LEITGEB (18).

In Marantaceae in ENGLER and PRANTL (11*c*) and by DUVAL-JOUVE (9).

LITERATURE CITED

1. BALFOUR, BAYLEY, On the genus *Halophila*. Trans. Bot. Soc. Edinburgh 13:290–343. *pls. 8–12*. 1879.
2. CASPARY, ROBERT, Die Hydrilleen (Anacharideen Engl.). Jahrb. Wiss. Bot. 1:377–513. *pls. 35–39*. 1858.
3. COSTANTIN, J., Recherches sur la structure de la tige des plantes aquatiques. Ann. Sci. Nat. Bot. VI. 19:287–331. *pls. 14–17*. 1884.

4. COURCHET, M., Étude anatomique sur les Umbellifères et sur les principales anomalies de structure que présentent leurs organes végétatifs. Ann. Sci. Nat. Bot. VI. **17**:107–128. *pls. 10–12*. 1884.
5. CUNNINGTON, HILDA M., Anatomy of *Enhalus acoroides* (Linn. f.) Zoll. Trans. Linn. Soc. Bot. London **7**:355–371. *pl. 36. figs. 13*. 1912.
6. DEBARY, A., Comparative anatomy of phanerogams and ferns. Oxford. 1884.
7. DUVAL-JOUVE, J., Sur quelques tissues de *Juncus* et de Graminées. Bull. Soc. Bot. France **16**:404–410. *pl. 3*. 1869.
8. ———, Same title. Bull. Soc. Bot. France **18**:231–239. *pl. 2*. 1871.
9. ———, Diaphragmes vasculifères des Monocotylédones aquatiques. Mém. Acad. Sci. Montpellier **8**:157–176. *pl. 8*. 1871.
10. ———, Histotaxie des feuilles de Graminées. Ann. Sci. Nat. Bot. VI. **1**:294–371. *pls. 16–19*. 1875.
11. *a*) ENGLER, A., and PRANTL, K., Natürlichen Pflanzenfamilien. Pt. III. **7**:226–237.
b) ———, *Idem*, Pt. III. **2**:12.
c) ———, *Idem*, Pt. II. **1**:1–6.
12. FALKENBERG, P., Vergleichende Untersuchungen über dem Bau der Vegetationsorganen der Monocotyledonen. Stuttgart. 1876.
13. GOEBEL, KARL, Pflanzenbiologische Schilderungen. Pt. II. 115–266. 1891.
14. ———, Über Regeneration im Pflanzenreich. Biol. Centralbl. **22**:385–397, 417–438, 481–505. *figs. 1–21*. 1912.
15. HABERLANDT, G., Physiologische Pflanzenanatomie. 3d edition. Leipzig. 1904. pp. 246–260, 388–395.
16. HARTWICH, C., und WINCKEL, M., Über das Vorkommen von Phloroglucin in Pflanzen. Arch. Pharmazie **242**:462–475. 1904.
17. LE BLANC, M., Sur les diaphragmes des canaux aérifères des plantes. Rev. Gén. Bot. **24**:233–243. *pl. 10*. 1912.
18. LEITGEB, H., Die Luftwege der Pflanzen. Sitzungsber. Kais. Akad. Wiss. Wien **18**:334–363. *pl. 1*. 1857.
19. MANGIN, L., Sur les composés pectiques. Jour. Botanique **7**:329. 1893.
20. MEYEN, FRANZ J. F., Phytotomie. Berlin. 1830. pp. 85, 193–206.
21. ———, Neues System der Pflanzenphysiologie. Berlin. 1837. pp. 294–309.
22. MONTESANTOS, NIKOLAUS, Morphologische und biologische Untersuchungen über einige Hydrocharideen. Flora **105**:1–32. *pls. 1–5*. 1912.
23. SAUVAGEAU, C., Sur la présence de diaphragmes dans les canaux aérifères de la racine. Compt. Rend. **106**:78–79. 1888.
24. ———, Sur la feuille des Hydrocharidees marines. Jour. Botanique **4**:269, 289, 295. *figs. 3*. 1890.
25. ———, Observations sur la structure des feuilles des plantes aquatiques, *Zostera*, *Posidonia*, *Cymodocea*, etc. Jour. Botanique **4**:41, 68, 117, 129, 173, 181, 221, 237. 1890.

26. SAUVAGEAU, C., Sur la structure de la feuille des genres *Halodule* et *Phyllospadix*. Jour. Botanique **4**:321–332. *figs. 7*. 1890.
27. ———, Sur les feuilles de quelques Monocotylédones aquatiques. Ann. Sci. Nat. Bot. VII. **13**:103–296. *figs. 64*. 1891.
28. SCHACHT, HERMANN, Physiologische Botanik. Die Pflanzenzelle, der innere Bau und das Leben der Gewächse. Berlin. 1852. pp. 70, 166.
29. SCHENCK, HEINRICH, Vergleichende Anatomie der submersen Gewächse. Bibl. Bot. **1**: 1887.
30. SCHWENDENER, S., Das Mechanische Princip im anatomischen Bau der Monocotyledonen. Leipzig. 1874. pp. 89–92.
31. SOLEREDER, HANS, Systematische Anatomie der Dicotyledonen. Stuttgart. 1899.
32. ———, Systematisch-anatomische Untersuchungen des Blattes der Hydrocharitaceen. Beih. Bot. Centralbl. **30**:24–104. *figs. 53*. 1913.
33. TRIMBLE, HENRY, The tannins. 1892.
34. TSCHIRCH, A., Angewandte Pflanzenanatomie. Vol. I. Wien u. Leipzig. 1880. pp. 428–431.
35. UNGER, FRANZ, Grundlinien der Anatomie und Physiologie der Pflanzen. Wien. 1866.
36. WIESNER, J., and MOLISCH, H., Untersuchungen über die Gasbewegung in der Pflanze. Sitzungsber. Kais. Akad. Wiss. Wien **98**:670–713. 1889.
37. WEISS, G. A., Anatomie der Pflanzen. Wien. 1878. pp. 295–306.
38. WORSDELL, W. C., On transfusion tissue: its origin and function in the leaves of gymnospermous plants. Trans. Linn. Soc. London. Bot. II. **5**:301–319. *pls. 23–26*. 1892.

FASCIATION

M. A. Brannon

(WITH SEVEN FIGURES)

During the spring of 1910, while an examination of a tree claim near Larimore, North Dakota, was being made, there were discovered some pronounced cases of fasciation. The tree claim had been planted to cottonwoods and willows in 1885. During the winter of 1909 the owner had taken considerable fuel from the northern portion of this grove of vigorous trees. In the summer of 1909 a large number of sprouts came from the stumps of the

FIG. 1.—A portion of the original timber claim and three years' growth of the cut-over region adjoining.

trees which had been removed (fig. 1). The number of sprouts was variable on different stumps, but in all cases the growth was pronounced and occasionally it was extreme, some of the sprouts having reached a height of two or three meters. On all of the stumps of the cottonwoods and on some of those of the willows one or more fasciated sprouts appeared. The flattening was particularly marked near the outer extremities of the stem, and was accompanied generally by profuse branching and forking of the fasciated specimens. The most superficial markings on the

fasciated sprouts were prominent cortex ridges along the whole axis of the young plant. Fig. 2 shows the relative size and the shape of the cortex ridges and also the flattened xylem and pith in a transverse section of modified cottonwood stem. This section

FIG. 2.—Transverse section of a fasciated cottonwood stem one year old; ×8; the notable cortex ridges and change of symmetry in the cross-section of the stem are well illustrated by these sections.

shows that pith, xylem, phloem, and cortex maintain the same relative positions in the abnormal specimens that they have in the normal cottonwood stem. The two exaggerated features of these flattened stems are the huge cortex ridges and the modification of radial symmetry.

The phenomenon of fasciation is not rare among plants, though it is not often reported for those having woody stems. Manifestly, the disturbing features, whatever they may be, which produced "banding" or "bundling" must have been considerably more pronounced in the wooded stems of cottonwoods, ash, willow, and other woody plants than they are in herbaceous stems of seedlings of pumpkin, young stems of thistles, floral axes of coxcomb, stems of asparagus, and other fasciated herbs.

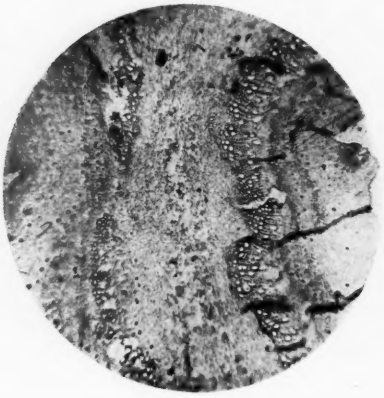


FIG. 3

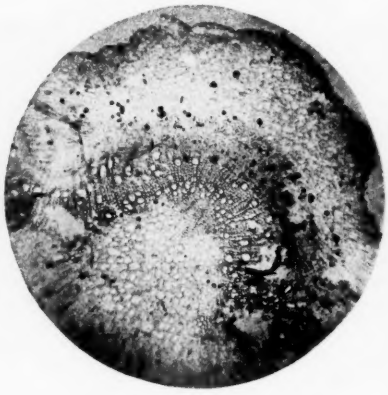


FIG. 4

FIGS. 3, 4.—Parts of the stem section showing the relation of the cortex ridges with phloem, xylem, and pith; ×13; fig. 4, section showing more clearly the relation indicated in fig. 3; ×25.

The number of atmospheres of pressure requisite for the flattening of a wooded stem corresponding to the cottonwood shown in the accompanying section (figs. 3 and 4) has not been determined. It is evident, however, that an enormous molecular disturbance would be required in order to change the molecular arrangement which caused the disturbance of radial symmetry of these woody stems. In seeking for the cause of the energy release which was expressed by this modification of symmetry, one naturally inquires into the chemical and physical factors involved. With reference to the chemical factors it seems evident that the stumps of the cut-away trees did not contain other compounds than those which

had been moving freely through the tissues of the tree while it was standing. There might have been larger quantities of various chemical substances per unit of living tissue, but hardly a different quality than that present in the uncut cottonwoods and willows. The soil had not been disturbed; there had been no change in drainage, and no great variation of precipitation during the latter months when the trees were standing and during the time that the fasciated sprouts had been developed. This seemed to indicate that, so far as the causes of fasciation in the stems of cottonwood and willow were concerned, it was necessary to seek them among physical rather than among chemical factors. From the list of physical factors such as light, gravity, and turgor it was easily possible to select turgor as the one which would be variable in the meristematic tissue near the exposed surface of the tree stumps out of which numerous sprouts developed. Root pressure of the cottonwood and willow plants was apparently in full operation during the early spring months after the trees had been cut away. The full flow of sap was directed into the meristematic tissues of the stumps from which a few buds developed in the early spring. This seemed the probable cause in the production of the phenomenon of cottonwood and willow fasciation.

Traumatism may have been involved in the changes registered in the young, rapidly growing sprouts. However, this seemed improbable, inasmuch as numerous sprouts were wholly free from fasciation, notwithstanding the fact that some of the more pronouncedly fasciated sprouts came from the same stumps on which normal sprouts were growing. Transition from the abnormally fasciated to the normal radial symmetry was evidenced by the most strongly fasciated sprouts after three seasons of growth. Figs. 5 and 6 show the bases of cottonwood saplings which had sprouted from the stumps four years before. The wide scar near the base of each fasciated specimen clearly indicated the location of a ruptured cortex which took place in the deeply furrowed fasciated specimen during its second season's growth. The dimensions of the cross-section of the base of the specimen shown in fig. 5 were 6 by 4.5 cm. Fig. 6 shows the base of a fasciated stem whose cross-section 15 cm. from the ground was 6.5 by 5 cm.

Fig. 7 shows a stem whose cross-section 25 cm. from the ground was 11×9.5 cm. These variations in symmetry were gradually

FIG. 5

FIG. 6

FIG. 7

FIGS. 5–7.—Basal lateral views of the sprouts three years after the beginning of fasciation, illustrating separation of cortex from woody cylinder and consequent exposure of wood to weather.

lost, and practically disappeared in fasciating sprouts at the end of three years' growth. Nearly all of the specimens which had such manifest banding and bundling during their first three years

of growth had changed to symmetrical cylinders having practically no evidences of fasciation beyond the terminal portion of the third season's growth. The uniform diameter in all parts of the stem produced during the fourth year, together with its smooth, firm bark, presented a great contrast to the unsymmetrical, fluted cortex produced during the three previous seasons. Seemingly the distribution of stress and the physical and chemical factors had reached stages similar to those which prevail in the production of normal cylindrical stems.

HUS[1] states that fasciation may be produced experimentally in annuals (*Phaseolus multiflorus* and *Vicia Faba*). The stems of these annuals fasciated when they were cut off directly above the cotyledons, and the roots fasciated when the tips were amputated or split. HUS also showed in work carried on at the Missouri Botanical Garden that plants with an indeterminate inflorescence would fasciate when treated as follows:

> About the time of the appearance of the first flowers the plant is kept as dry as possible, only enough water being given to prevent wilting. As a result, the flowering period will be comparatively short, and, in an indeterminate inflorescence, the buds near the end of the spike remain undeveloped. If at that time the plants are daily abundantly irrigated, occasionally with manure water, numerous fasciations will make their appearance, but it must be remembered that this result is usually reached only with plants which throughout their existence have been well nourished and well cared for generally. For no apparent reason, one plant will fasciate, while the next one belonging to the same species remains normal.

From this and other experiments, HUS concludes that GOEBEL is correct when he affirms that fasciation results from the rapid introduction of sap into stems which would not normally have fasciated. This conclusion was further supported by experiments carried on at Berkeley, California, in September 1904. Within a week after a heavy rainfall a very large number of teratological cases appeared. They were represented by fasciations, by torsions of the stem, petalody of the stamens, phyllody of the pistils, and prolongations of the axis through the center of the flower, known as frondiferous diaphysis. HUS further cites the experiences of

[1] Mo. Bot. Gard. Report, 1906, pp. 147–152.

some asparagus growers in California, who testified that there was a greater percentage of fasciated shoots in their beds of asparagus during the period when the first stems pierce the soil, especially after a cold winter.

DEVRIES conducted experiments[2] in his garden at Amsterdam, and minutely studied fasciated plants in their natural conditions. From the experiments and observations he agrees heartily with GOEBEL that fasciation is due to internal stimuli, notably increasing pressure of cell sap.

The whole question of monstrosities might be ignored but for the light their study throws upon numerous morphological structures among plants. To illustrate some of these morphological problems the lists of floral parts which are closely united have been cited. In the whorl of microsporophylls one often finds a complete union of the filaments, also the fusion of megasporophylls in the formation of compound ovaries; the fusion of the petals in the gamopetalous corolla, as for instance in the orchids; the fusion of seed coats in cycads; the fusion of nucellus and integuments in some of the other gymnosperms; the fusion of the bract with the axillary flowering stock in basswood (*Tilia americana*); and the union of the calyx with the ovary as in the apple and other pomaceous fruits. This group of morphological modifications was classified as negative by WORSDELL.[3] The same author classifies as positive congenital increase of parts the following: the pappus or the sepals in the Compositae; twin embryos which develop from a single egg that divides vertically perhaps instead of transversely; and twin flowers which arise by the modifications of the apical region of growth.

WORSDELL holds that, in addition to these congenital fusion problems, there are those which may be called post-genital; for example, the plantain with twin spikes of flowers at the summit of the stem, the *Campanula* with four flowers borne at the apex of an abnormal stem, the leaves of the *Oxalis* sometimes individual instead of being in three parts as is customary, the fusion of the flowers in *Crocus*, and lastly fasciation itself. In support of his view that the various monstrosities in plants are sometimes con-

[2] Die Mutationtheorie 2:541. 1903.

[3] New Phytol. 4:55–74. 1905.

genital and sometimes post-genital, he has recourse to a theory of CHURCH, who holds that "growth is distributed at the apex of a shoot in such a manner that its transverse component may be expressed by a plane, circular construction around a circular point (the growth center), and the circular section of the vast majority of plant axes is evidently the outcome of such a regular and symmetrical distribution from the growing point." WORSDELL approves of CHURCH'S theory that central distribution is distributed around several points instead of about one center of growth. He holds that some growth centers are weaker than others, hence develop less in diameter and elongate more slowly, and this produces torsion, which is an almost invariable component of fasciation. Having developed this theory of centers of growth in different radii of the apical region of a stem, he holds that any force which upsets the equilibrium of the organism will tend to bring about a reversal to ancestral conditions. In other words, cylindrical woods like those of our cottonwood and ash, upon losing their balance, will repeat the long-past experience of lycopods, ferns, and algae, where branching primarily is probably in one plane.

WORSDELL furthermore treats of plant monstrosities as a possible pathological condition. He refers to it as a subtle diseased condition brought about by superabundant nutrition that destroys the balance of the organism and produces hypertrophy of parts. It is pointed out that the crested form of *Celosia argentea* is not produced abundantly without manuring the potted plants. WORSDELL'S conclusion is that there are morphogenetic principles underlying the phenomenon of fasciation. He holds that fasciation is to be explained as a resultant of the more or less equal conflict waged between two opposing tendencies or forces, one of which induces integrity of parts of a plant and the other induces plurality of parts.

In a recent discussion, WHITE[4] reviews interesting genetic studies based upon a fasciated variety of *Nicotiana Tabacum*. The race of these fasciated specimens was obtained from the self-fed seed of a mutant found growing in a field of Cuban tobacco. He

[4] WHITE, O. E., The bearing of teratological development in *Nicotiana* on theories of heredity. Amer. Nat. **47**:216–228. 1913.

suggests that these studies indicate that "the gene for fasciation appears to me to lie deeper in sporogenesis than the chromosome." "The abnormal character development appears most easily interpreted from a physiological standpoint." Whether or not his contention is correct that "physiological" factors rather than chromosomes control the continuous fasciation through the chain of alternation of generations, there can be no question, however, regarding the fact that some physiological factor, notably sap pressure, is intimately associated with the control of the fasciation of ash, willow, and cottonwood on stems found on tree stumps in the North Dakota tree claim.

The examples of fasciation presented in this paper have been noted because of the bearing which the study of abnormal structures may have upon the study of normal morphological structures; and also because of the possible interesting physiological relation existing between increased sap pressure and the disturbed balance of forces which are believed to be responsible for cottonwoods and willows undergoing a change from radial to more or less bilateral symmetry of stem during their first three seasons of growth.

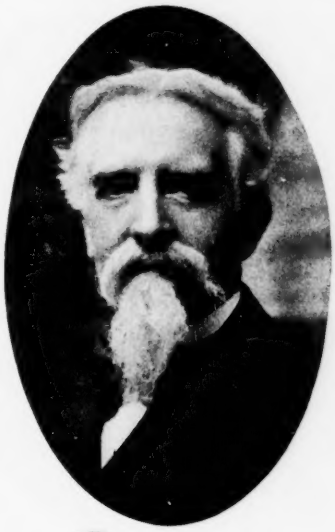
UNIVERSITY OF IDAHO
MOSCOW, IDAHO

BRIEFER ARTICLES

PHILIPPE EDOUARD LEON VAN TIEGHEM

(WITH PORTRAIT)

The younger generation of botanists perhaps does not realize the important part played by VAN TIEGHEM in the progress of botany. In recent years his publications, chiefly in the *Annales des Sciences Naturelles*, have had to do with the anatomical details of various families. Such work attracts very little attention in these days. In 1886, however, when VAN TIEGHEM and DOULIOT published the paper entitled "Sur la polystélie," a new epoch in the history of anatomy was introduced. It was the first formal statement of the stelar theory, as we have had it ever since. Before that time the section of a stem was described as consisting of "fundamental tissue" which vascular strands traversed in various ways. In other words, pith, medullary rays, and cortex were all regarded as regions of the same tissue. It may be said in passing that this old conception is still current in certain texts. It was VAN TIEGHEM'S good fortune to present first the fact that the stele is an entity, quite distinct from the cortex. Curiously enough, the conception of the polystele presented in the original thesis has disappeared, and the rest of the stelar terminology of VAN TIEGHEM has been set aside, but the conception remains.



Ph. van Tieghem

VAN TIEGHEM was born in 1839 at Bailleul. In 1879 he was appointed Professor of Botany at the Museum of Natural History (Paris), and

from that time until his death, on April 28, 1914, he held the most commanding botanical position in France. His influence upon the botany of France, on account of the peculiarly intimate official relations of French universities, was greater than that of mere reputation as a botanist. He became botanical editor of the *Annales des Sciences Naturelles* in 1882, succeeding DECAISNE in that position. Perhaps his most extensive and most used volume was the *Traité de botanique*, published in 1884, but most referred to in connection with the second edition, published in 1891.—J. M. C.

RETENTION OF CHLOROPHYLL THROUGH THE PARAFFIN PROCESS

In order to study the chloroplasts in corn plants showing various types of reduction of chlorophyll content, the following method was devised to retain the chlorophyll through the paraffin process. The material is fixed in a saturated solution of barium hydrate for 12–24 hours, washed with water, dehydrated with alcohol, dealcoholized with xylol, and imbedded in paraffin. The material should be kept in the dark and dehydrated rather rapidly. This method may also be used for imbedding in celloidin. The details of the methods as stated here are purely arbitrary, and may no doubt be modified with advantage. If a weaker fixing solution is used, it must be handled with great care, as barium hydrate precipitates readily as barium carbonate on exposure to carbon dioxide. If a stronger solution is desired, barium hydrate may be dissolved in an ammonium chloride solution.

Acknowledgments are due Professor R. A. EMERSON, of Cornell University, at whose suggestion the investigation was undertaken.—
E. G. ANDERSON, *University of Nebraska.*

CURRENT LITERATURE

BOOK REVIEWS

Bacteriology

The Book of Books somewhere states that a man is not to be heard for his much speaking; inferentially, one surmises that quality is to be more highly esteemed than quantity, and doubtless this may be regarded as holding equally true in the making of books. In the book under review,[1] Professor REED has done well, very well, in this respect, without brevity in the least way marring the quality of the subject-matter presented to his readers.

The preface to a book may frequently be regarded as a mirror of the mind of an author, for therein is displayed the purpose that prompts the writing of the book. So it was with pleasure that the reviewer noted the following phrase: "Wherever possible the experiments are planned to give quantitative results, to the end that vagueness of statement and uncertain thinking may disappear." Were this idea more frequently found expressed and acted upon in "books for students," fewer puny guides to wisdom would be found in the hands of students in our laboratories.

The manual is divided into 16 sections, and in addition 16 appendices. The sections deal with the form and occurrence of bacteria; the nutrition of bacteria; sterilization of culture media; relation of bacteria to factors of physical environment; relation of bacteria to biological factors; methods of culture, isolation, staining, and routine study of bacteria; qualitative and quantitative studies of bacteria of water and sewage, of soil, and of milk; the bacterial diseases of man and animals, and of plants; and fermentation studies. The appendices are framed with the idea of presenting in a handy fashion important matter that otherwise would be scattered in various places throughout the text. Therein are noted descriptions of the most recent methods and applications of sterilization, handling of stock cultures, making of permanent museum preparations, of titration, of chemical determinations of ammonia, nitrate, nitrite, of total nitrogen, of reducing sugars; conversion tables; alcohol computation tables; and the like. In appropriate places throughout the exercises are references to textbooks, monographs, and papers in the current literature of the subjects under discussion, a most important feature not infrequently omitted by authors.

Excellent as the presentation is in most respects, the reviewer does not find himself in perfect accord with the author in certain instances; for example,

[1] REED, HOWARD S., A manual of bacteriology for agricultural and general science students. 8vo. pp. 179. *figs. 46*. Boston: Ginn & Co. 1914.

in the section allotted to diseases of man and animals the impression is produced in section 132 that the use of mercuric chloride is too lavishly recommended. It has its place, but would it not be better to advocate the sterilization of such cultures as those of anthrax and tuberculosis by means of the autoclave? Then, too, it would have been well to have inserted some special admonitory warnings in introducing the student to the study of anthrax and tuberculosis.

Attention might be directed to an error in the description of carrying out the technic of WELCH'S capsule stain (p. 36); water in no instance ought to be allowed to come in contact with the film, all washing should be done with 0.85 per cent sodium chloride solution. In exercise no. 27, the presentation of the formula of ELSNER'S potato gelatine medium would appear to be misleading, inasmuch as this medium is not one suitable for the growth of bacteria in general; in fact, the reverse is true, as ELSNER introduced it in 1896 for the purpose of providing a selective medium for the typhoid bacillus and preventing the growth of other bacteria associated with it in such materials as feces, urine, water, etc. The reaction as given is evidently a misprint for "plus 0.25." An unfortunate error is given prominence in Appendix E, wherein it is stated in paragraphs five and six that the term "plus(+)1.0 is equivalent to 1.0 cc. of normal hydrochloric acid per *liter*"; on the contrary, it should read 1.0 cc. *per cent* (see *Standard methods of water analysis*, 2d ed., 1912, p. 126).

Apart from the foregoing criticisms, and judged upon its merits, the manual is admirably adapted, not alone for students of agriculture and of the technical sciences, but for students of any institution where bacteriology is worthily taught in its broader and more fundamental aspects. The book is of a handy size, well printed, attractively bound, and adequately illustrated.—N. MACL. HARRIS.

The marine algae of Iceland

The Danish botanists, largely through the inspiration of WARMING, having completed in satisfactory form the botanical investigation of the Faeröes, have turned attention to Iceland, as the Danish dependency now most in need of study. The first paper of the Iceland series is the work of Dr. HELGI JÓNSSON[2] of Reykjavik, Iceland, and it gives an elaborate account of the marine algae which are so richly represented on the coast of that far northern island. There are 200 species listed, of which 76 are reds, 67 browns, and 51 greens. In the chapter on life-conditions, the subjects treated are the nature of the coast; the movements, temperature, and salinity of the water; atmospheric temperature and humidity; precipitation; wind; and light. As usual elsewhere, the algae are best developed on rocky coasts. The practical upper limit of algae is reached at the flood level of neap tides.

[2] ROSENVINGE, KOLDERUP, L., and WARMING, E., The botany of Iceland. I. The marine algal vegetation by HELGI JÓNSSON. pp. 186. *figs.* 7. Copenhagen: J. Frimodt. London: John Wheldon & Co. 1912.

The body of the work deals with the horizontal and vertical distribution of the species. Of the 200 species, 11 only are rated as arctic, whereas 81 are termed subarctic, and 108 boreal; of the last, 12 are even warm boreal species extending south to the Mediterranean. In considering the vertical distribution, JÓNSSON terms the upper part of the shore, from the upper limit of algal growth to the low-water mark of neap tide (almost coinciding with the lower limit of the Fucaceae), the upper littoral zone. The lower littoral zone extends from here to the usual low-water mark of spring tide. Then begins the vegetation that is constantly submerged. In the upper littoral zone there are 18 reds, 18 browns, 36 greens, and 6 blue-greens; the great bulk of the vegetation, however, is composed of browns. Furthermore, 13 of the reds in the upper littoral zone occur in shaded clefts, being proper to lower zones. In the lower littoral zone there are 39 reds, 37 browns, and 17 greens; the relationship of these is much closer to the submerged species than to the upper littoral species. Of the submerged or sublittoral species, 39 are reds, 22 browns, and 3 greens. It is possible that algae may occur as far down as 80 meters, but they are not abundant below 60 meters. A third of the work is devoted to a detailed account of the numerous algal associations of the three zones noted above, the littoral associations being subdivided into those of the light and of the shade.

This valuable treatise closes with some notes on the duration of algae and periodical changes. The perennial algae, such as *Fucus* and *Laminaria*, have only a very short period of rest, in spite of the long winter; some species hardly rest at all. *Pelvetia canaliculata* vegetates and fruits the year around.—H. C. COWLES.

Postglacial changes in German vegetation

HAUSRATH,[3] professor of forestry at Carlsruhe, has issued an extremely useful little book, which gives in compact form a summary of our knowledge regarding landscape and vegetation changes in Germany since the Ice age. One of the author's chief objects is to explain the present landscapes in terms of past conditions. To give proper orientation to the reader, HAUSRATH presents in brief fashion the ordinary fundamentals of phytogeography, noting the various factors and formations that are in evidence in Germany. It is interesting to note that nearly half the land of Germany is cultivated, one-quarter forest-covered, and one-sixth pasture and meadow. The various views concerning the climate of the Ice age and of subsequent times from the Ice age to the days of the Romans are well set forth, as are the probable stages in the re-establishment of vegetation immediately following the retreat of the glaciers. A chapter is devoted to changes subsequent to Roman occupation,

[3] HAUSRATH, HANS, Pflanzengeographische Wandlungen der deutschen Landschaft. Wissenschaft und Hypothese XIII. pp. vi+274. Leipzig: B. G. Teubner. 1911. *M* 5.

and there are here depicted the early periods of forest destruction, the fluctuations in forest area associated with peace and war, and the growth of the ideas of conservation and afforestation. The closing chapters consider changes in the composition of forests and the problems of heaths and moors, which are discussed from the viewpoint of origin, of destiny if left to themselves, and of utilization by man. The great merit of this volume lies in its strongly dynamic attitude, an attitude that cannot be too highly commended in all phytogeographic work.—H. C. COWLES.

The trees of Belgium

MASSART[4] has issued a profusely illustrated little book on the trees of Belgium, his object being to present the subject so as to interest intelligent lovers of the woods, rather than to make a manual for botanists or foresters. The book is in no sense designed as a manual of identification, but rather it presents the interesting problems about which the nature-lover is likely to inquire. In the first portion of the book MASSART considers wood structure and tree architecture. Then follows a section on the relation between trees and soil, and a similar section on the relation between trees and the atmosphere. The final section presents the life-history of trees, dealing with birth, competition, decrepitude, and death. In the chapter on tree architecture, the author discusses deliquescent and excurrent trees, regeneration of injured terminal and lateral branches, the influence of isolation on the shape of the crown, and enlarged trunk bases. The section on soil relations considers the distribution of trees (an excellent detailed map of the Belgian woodlands accompanies this), the influence of the soil on trees, and the influence of trees on the soil; among the topics treated under the latter heading are rock disintegration, fixation of dune sand, and chemical changes in the soil. In the final section much attention is paid to tree diseases and insect pests. It is a pity that we do not have many similar books to accommodate the rapidly increasing army of nature-lovers.—H. C. COWLES.

NOTES FOR STUDENTS

The vegetation of the Nebraska sandhills.—The average traveler regards the prairies and plains as regions of extreme monotony; particularly is this true if his way takes him through a region of sandhills. The total incorrectness of this view is admirably illustrated by the publication of POOL'S researches in the Nebraska sandhills.[5] From an earlier and semipopular presentation

[4] MASSART, J., Nos arbres. pp. viii+214. *figs. 238. map 1.* Brussels: Henri Lamertin. 1911.

[5] POOL, RAYMOND J., A study of the vegetation of the sandhills of Nebraska. Minn. Bot. Studies, III. 4:189–312. *pls. 15. figs. 16. map 1.* 1914.

by the same author[6] we had learned to know something of the fascination and scientific interest of these dynamic landscapes, and now we have his detailed results.

The Nebraska sandhill country covers an area of about 18,000 square miles, that is, nearly one-fourth of the area of the state. There are similar but smaller areas of sandhills in Kansas, Colorado, and the Dakotas. The soil is composed of dune sand, probably derived from the Loup Fork (Tertiary) beds. These hills seem to have been formed largely at some previous epoch and to have become stabilized and occupied by vegetation. Through the influence of man, mostly on account of prairie fires and overgrazing, many of these ancient dunes have become rejuvenated to the detriment of those responsible for it.

After giving the results of his careful measurements of wind, rainfall, evaporation, temperature, and other ecological factors, POOL takes up in detail the vegetation of the region. It is a pleasure to note the author's caution in using the word "formation." He rightly believes in using this term only for large units, referring the "formations" of many authors to associations. The characteristic upland formation is the prairie-grass formation, which is contrasted sharply with the short-grass formation of the plains, the two embracing most of the great climatic grasslands between our eastern forests and the mountains. These two great formations have similar physiognomy but different component species; the limiting factors are the available water and competition, and not temperature, as supposed by MERRIAM. The chief association is the bunch-grass association, dominated especially by *Andropogon scoparius;* this is the vegetation that prevailed generally before the advent of the white man, and is regarded as the temporary climax of the region. The vegetation of this association is open, the grasses occurring in tufts or bunches, but it is supposed that ultimately some closed prairie-grass association will prevail. There is evidence of this in the spear-grass association (dominated by *Stipa comata* and *Koeleria cristata*), and farther west in the grama buffalo-grass association (dominated by *Bouteloua* and *Bulbilis*).

Doubtless the most interesting features of the sandhills are the blow-outs. These are retrogressive features and are due, as noted above, especially to prairie fires and overgrazing. At first, through the death of the plants there are small patches of bare sand. Later the sand is scooped out by the wind, forming conical or crateriform depressions, known as blow-outs. As the sand is scooped out, more sand falls in from the sides, so that the blow-out is increased in circumference, as well as in depth. Extreme cases are recorded where the depth may be as much as 100 feet and the circumference 600 feet. When wind erosion becomes checked, vegetation again gets a foothold, the chief

[6] POOL, RAYMOND, J., Glimpses of the Great American Desert. Pop. Sci. Monthly **80**: 209–235. *figs.* 17. 1912.

pioneers being *Calamovilfa longifolia*, *Psoralea lanceolata*, and *Redfieldia flexuosa*. After a time these pioneers are followed by the bunch-brass association; after this vegetational changes are much less rapid. One of the chief features of interest in the woodland formations along the streams is the overlap of the deciduous eastern forest and the yellow pine (*Pinus ponderosa scopulorum*) forest of the west. The lowland formations are much like those elsewhere both as to content and succession, except that a meadow type represents the temporary climax; probably one of the more eastern of the prairie-grass associations represents a more ultimate condition.—H. C. COWLES.

The water-balance of desert succulents.—The Sonoran desert is very rich in succulents which carry a large water-balance. Some of the most striking of these have been studied in detail for some years at the Desert Laboratory.[7] Mrs. SPALDING had previously shown that the stems of *Cereus giganteus* expand and contract in a most remarkable manner, as water is accumulated or lost.[8] These movements are readily measured by noting the variations in distance between the ridges from time to time. Mrs. SPALDING, as her part of the contribution, reports greatly extended experiments along this line on the same and on additional species. The earlier work has been confirmed in practically all respects. In addition to the influence of soil water in changing the plant form, insolation is found to be an important secondary factor; for example, the furrows on the south sides of stems are narrower than those on the north sides. The behavior of *Echinocactus Wislizeni* is much like that of *Cereus giganteus*, but in *Opuntia* the behavior is simpler, consisting merely of the swelling and shrinking of the stem segments.

MACDOUGAL'S part of the work consisted of a study of variations in the water-balance, due to seasonal moisture fluctuations and other causes. The remarkable ability of these desert succulents to tide over long periods of drought is brought out in striking fashion in the case of plants of *Cereus giganteus*, in which branches have remained alive and even have bloomed a year after the main trunk bearing them has died. More efficient even than the cacti is *Ibervillea sonorae*, a plant whose stem base is tuberized. For ten years tubers of this species have remained alive, without a renewal of water supply, sending up short green stems each summer; during this time but half of the original weight had been lost. In the general conclusions attention is called to great differences in individual behavior under similar experimental conditions. The

[7] MACDOUGAL, D. T., and SPALDING, E. S., The water-balance of succulent plants. Carnegie Institution of Washington, Publication 141. *pp. 77. pls. 8.* 1910. See also MACDOUGAL, D. T., The water-balance of desert plants. Ann. Botany **26**:71–93. *pls. 5.* 1912.

[8] SPALDING, E. S., Mechanical adjustment of the Sahuaro (*Cereus giganteus*) to varying amounts of stored water. Bull. Torr. Bot. Club **32**:57–68. 1905; see BOT. GAZ. **40**:396. 1905.

decline in evaporation each year in plants whose water supply is not replenished is attributed in part to increasing concentration of the cell sap; in the cacti this increase was from 1 to 3 per cent. From 60 to 70 per cent of the maximum water-balance may be lost by cacti without impairing the power of recovery and subsequent growth. It is suggested that a detailed chemical study of these plants is needed, it being felt that their high osmotic activity and their great acidity resulting from modified photosynthesis are insufficient to explain the origination of the habit of accumulating and retaining large water-balances.—H. C. COWLES.

English woodlands.—As would be expected, very few of the English woodlands are primeval. Such woodlands may still be found, however, near the upper forest limits in mountainous regions.[9] Most English woodlands are to be regarded as semi-natural, that is, the trees are felled somewhat regularly, but the reproduction, either from seeds or suckers, is natural. New forest plantations are distinguishable from natural or semi-natural woodlands by the presence at times of exotic tree species, and almost always by the absence of a representative woodland ground flora. Three main series of woodlands are recognized, the alder-willow series of wet soils, the oak-birch series of siliceous soils, and the beech-ash series of calcareous soils. The series are further divided into associations.

ADAMSON has made an intensive study of Gamlingay Wood in western Cambridgeshire, one of the semi-natural woodlands noted above.[10] The wood is on bowlder clay, part of which is calcareous and part non-calcareous; the trees on the former are oak and ash, while the ash is absent on the latter. Although it is noted that there are intergradations, it is observed that the herbage in the two woodland types is different; the dominant forms in the siliceous woodland are *Pteris aquilina* and *Holcus mollis*, whereas those of the calcareous woodland are *Spiraea Ulmaria*, *Mercurialis perennis*, *Deschampsia caespitosa*, and *Fragaria vesca*. Little attention is paid to successional features. It is believed by the reviewer that more thorough successional studies would tend to break down some of the distinction between calcareous and siliceous woodlands, as recognized by English ecologists; it seems almost certain that an original underlying soil must more and more lose its influence on vegetation, as humus accumulates. Careful studies were made by ADAMSON of evaporation, soil moisture, and other factors.

In connection with the above it may be noted that TANSLEY and ADAMSON[11] have given an account of some observations made in some Gloucestershire

[9] MOSS, C. E., RANKIN, W. M., and TANSLEY, A. G., The woodlands of England. New Phytol. **9**:113–149. 1910.

[10] ADAMSON, R. S., An ecological study of a Cambridgeshire woodland. Jour. Linn. Soc. Bot. **40**:339–387. *pls. 6*. 1912.

[11] TANSLEY, A. G., and ADAMSON, R. S., Reconnaissance in the Cotteswolds and the Forest of Dean. Jour. Ecol. **1**:81–89. 1913.

woodlands. One of the most interesting features is a wood composed largely of box (*Buxus sempervirens*), possibly native to Britain.—H. C. COWLES.

Jurassic Osmundaceae.—SINNOTT[12] has investigated the structure of petrified stems of *Osmundites Dunlopi* from the Jurassic of New Zealand. They are characterized by a parenchymatous pith, with no internal phloem or endodermis, and leaf gaps are invariably present. In one specimen typical diarch roots, with a definite cortex, were observed in the pith, and it is concluded that the xylem elements described as forming part of a "mixed pith" in *O. Kolbei* probably represent root bundles. It is thought that the relationship between Zygopterideae and Osmundaceae cannot be close, since the anatomy of the leaf trace and foliar bundle in the two groups is so widely different. It seems evident that there were both protostelic and siphonostelic Osmundaceae during the Mesozoic, and there is no evidence that the protostelic forms have given rise to the siphonostelic ones.—J. M. C.

Welwitschia.—CHURCH[13] has made a detailed study of the strobili of *Welwitschia*, supplying facts and new illustrations that were much needed. The "flowers" having clearly been originally bisporangiate, much attention is given to reduction phenomena, such as dicliny, the diminished number of members, etc. A good deal is made of "minimum construction" associated with a xerophytic type, observed in the perianth, the androecium, and gynoecium; but the statement is emphasized that "a minimum construction does not imply any phylogenetic relationship to other minimum types." The author finds no indication of any relation to the flowers of angiosperms.—J. M. C.

Relationships of Fagaceae.—Miss BERRIDGE[14] has investigated the flowers of certain Fagaceae, especially those of *Castanopsis chrysophylla*, comparing them with those of *Castanea vulgaris*, *Fagus sylvatica*, *Quercus Robur*, and *Juglans regia*. She takes issue with the common conclusion that the Amentiferae are an isolated group, with no obvious relationship to other angiosperms. She shows that the flower differs in no essential from other epigynous types of flowers, and compares in detail the flowers of Rosaceae and Cupuliferae, claiming that in all probability the epigynous Rosaceae are most nearly related to the ancestors of the Fagaceae.—J. M. C.

---

[12] SINNOTT, E. W., Some Jurassic Osmundaceae from New Zealand. Ann. Botany **28**:471–479. *pl. 37*. 1914.

[13] CHURCH, A. H., On the floral mechanism of *Welwitschia mirabilis* (Hooker). Phil. Trans. Roy. Soc. London B **205**:115–151. *pls. 9–13*. 1914.

[14] BERRIDGE, E. M., The structure of the flower of Fagaceae, and its bearing on the affinities of the group. Ann. Botany **28**:509–526. *figs. 9*. 1914.

GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

A

Adamson, R. S., work of 535
Aecidium cup, morphology and cytology of 1
Aggregate ray hypothesis 36
Alisma, delayed germination in 285
Amentiferae, anatomy of 36; reduction in 36
Amphoromorpha 249; **entomophila** 251
Anderson, E. G. 528
Angiosperms, phylogeny of 36
Antagonism, measurement of 272; quantitative criteria of 178
Antagonism curves, as affected by concentration 367
Antarctic vegetation 189
Antheridia, of Symphyogyna 407
Araucarioxylon 168, 375
Arber, E. A. N., work of 374
Archegonia, of Symphyogyna 406
Arthrostylidium angustifolium 277; multispicatum 278; sarmentosum 278
Ascomycetes, origin of 376
Association, bunch-grass 384, 388; Chrysothamnus-Sarcobatus 384, 395; Gutierrezia-Artemisia 385, 398; Hordeum jubatum 384, 395; lichen 384, 393; mat 384, 393; plains ruderal 385, 397; prairie-grass 384, 390; primitive bunch-grass 385, 397; salt-grass 385, 396; sand-hills mixed 384, 395; short-grass 383, 385; Stipa-Aristida 384, 394; swamp 384; wheat-grass 383, 387

B

Bacteriology, manual of 529
Bailey, I. W. 36
Bamboos, of Porto Rico 277
Bartlett, H. H., work of 191
Baumann, E., "Die Vegetation des Untersees" 449
Beattie, R. K., work of 192
Beer, R., work of 373
Belgium, trees of 532
Benecke, W., "Morphologie und Entwickelungsgeschichte" 86
Berridge, E. M., work of 536
Betulaceae, anatomy of 54
Beutenmüller, W., work of 95
Blackman, V. H., work of 280
Blakeslea 353; **trispora** 353
Borneo, British North 282
Boysen-Jensen, P., work of 89
Brachyoxylon 171
Brandegee, Katherine L., work of 376
Brandegee, T. S., work of 456
Brannon, M. A. 518
British North Borneo 282
British rusts 187
Brown, R. N. R., work of 189
Buller, A. H. R., work of 375

C

Caldwell, J. S., work of 280
Cameron, A. T., work of 375
Castanea dentata, anatomy of 54
Casuarinaceae, anatomy of 55
Cecidology 93
Chamberlain, C. J. 88, 375
Chandler, W. H., work of 451
Chantransiopsis 246; **decumbens** 248; **stipatus** 248; **Xantholini** 249
Chase, Agnes 277
Chlorophyceae, new 456
Chlorophyll, retention through the paraffin process 528
Chromosomes and sex 454
Church, A. H., work of 536
Coal Measure plants 374
Colorado, prairie vegetation of a mountain-front area 377
Comere, J., work of 281
Compton, R. H., work of 283
Congo flora 284
Contributors: Anderson, E. G. 528; Bailey, I. W. 36; Brannon, M. A. 518; Chamberlain, C. J. 88, 375; Chase, Agnes 277; Cook, M. T. 95; Coulter, J. M. 188, 189, 192, 283, 284, 337, 374, 375, 376, 450, 454, 455, 456, 528, 536; Cowles, H. C. 449, 451, 531, 532, 534,

535, 536; Crocker, W. 91, 285; Darsie, M. L. 101; Davis, W. E. 285; Deutsch, H. B. 100; East, E. M. 93, 191; Eckerson, Sophia H. 254; Elliott, Charlotte 101; Fromme, F. D. 1; Fuller, G. D. 98, 188, 190, 193, 281, 454, 455; Getman, M. R. 264; Greenman, J. M. 376; Harris, N. MacL. 350; Hill, J. B. 61; Holden, Ruth 168; Jeffrey, E. C. 322; Knight, L. I. 452; McAllister, F. 137; McCormick, Florence A. 401; Martin, J. N. 154; Osterhout, W. J. V. 178, 272, 367; Otis, C. H. 457; Peirce, G. J. 101; Roberts, Edith A. 432; Sharp, L. W. 373, 419, 452, 453; Sinnott, E. W. 36; Snow, Laetitia M. 495; Transeau, E. N. 282; Thaxter, R. 235, 353; Vestal, A. G. 377; Winton, Kate B. 445
Convallariaceae, embryo sac of 137
Cook, M. T. 95
Cordaitean wood 455
Coseleya 374
Cosens, A., work of 95
Coulter, J. M. 188, 189, 192, 283, 284, 337, 374, 375, 376, 450, 454, 455, 456, 528, 536
Cowiea 282
Cowles, H. C. 449, 451, 531, 532, 534, 535, 536
Cretaceous lignites 168
Crocker, W. 91, 285
Cruciferae, embryogeny of 284
Cupressinoxylon 172

D

Darbishire, O. V., work of 190
Darsie, M. L. 101
Davis, W. E. 285
Delayed germination in Alisma 285
Desert succulents, water-balance of 534
Deutsch, H. B. 100
Dewers, F., work of 90
Diaphragms of water plants 495
Dissophora 361; **decumbens** 361
Dodge, B. O., work of 376
Doncaster, L., work of 454

E

East, E. M. 93, 191
Eckerson, Sophia H. 254
Elkins, M. G., work of 455
Elliott, Charlotte 101
Embryo sac, of Convallariaceae 137; of Maianthemum canadense 140; of Medeola virginica 142; of Peperomia 374; of Polygonatum commutatum 143; of Smilacina amplexicaulis 140; of Smilacina sessifolia 139; of Streptopus roseus 141
English woodlands 535
Equisetum, sporogenesis in 373
Eremocitrus 192
Evaporation and soil moisture 193
Evolution, a theory of 91

F

Fagaceae, relationships of 536
Fagus grandifolia, anatomy of 49
Fasciation 518
Felt, E. P., work of 95
Fisher, G. C., work of 374
Flax fruit, histology of 445
Forestry in New England 188
Fresh-water algae, ecology of 281
Fresh-water flora 189
Fromme, F. D. 1
Fuller, G. D. 98, 188, 190, 193, 281, 454, 455
Fungus-parasites of insects 235

G

Gates, R. R., work of 191
German vegetation, postglacial changes in 531
Germination 101
Gerry, E., work of 283
Getman, M. R. 264
Gibbs, Lilian S., work of 282
Graham, Margaret, work of 453
Greenman, J. M. 376
Grove, W. B., "The British rust fungi" 187
Gwynne-Vaughan, D. T., work of 192

H

Haplosporangium 362; **bisporale** 363; **decipiens** 364
Harris, N. MacL. 530
Hauman-Merck, L., work of 98
Hausrath, H., "Pflanzengeographische Wandlungen" 531
Hawley, R. C., and Hawes, A. F., "Forestry in New England" 188
Heilbronn, A., work of 100
Hill, J. B. 61
Holden, Ruth 168
Holyoke range, plant successions of 432
Hormiscium **myrmecophilum** 238
Hormosira, oogenesis in 264
Howard, C., work of 93
Howard, R., work of 93
Hybrids, spore conditions in 322

I

Iceland, marine algae of 530
Icones Bogorienses 450
Immunity as a physiological test 455
Insects, fungus-parasites of 235
Isaburo-Nagai, work of 99

J

Java, orchids of 456
Jeffrey, E. C. 322
Jurassic Osmundaceae 536

K

Kidston, R., work of 374
Knight, L. I. 452
Kultur der Gegenwart 86

L

Lake Constance, vegetation of 449
Lee, E., work of 376
Leguminosae, comparative morphology of 154
Linum usitatissimum, histology of fruit 445
Livingston, B. E., work of 281
Lock, R. H., "Rubber and rubber-planting" 188
Lophoschoenus 282
Lotsy, J. P., work of 91
Lycopodium, anatomy of 61; Billardieri, anatomy of 75; carinatum, anatomy of 64; Holstii, anatomy of 77; Phlegmaria, anatomy of 68; varium, anatomy of 68; verticillatum, anatomy of 79

M

McAllister, F. 137; work of 452
McCormick, Florence A. 401
MacDougal, D. T., work of 534
Maianthemum canadense, embryo sac of 140
Marsh plants, xeromorphy of 450
Marsilia, spermatogenesis in 419
Martin, J. N. 154
Massart, J., "Nos arbres" 532
Medeola virginica, embryo sac of 142
Medicago sativa, morphology of 160
Mexico, new plants from 456
Mitosis, in Preissia 452; in Tetraspora 452; in Vicia 372
Moss, C. E., work of 535
Mosses, South African 284
Muiaria 241; **armata** 244; **gracilis** 243; **Lonchaeana** 244; **repens** 245
Muiogone 230; **Chromopteri** 239
Multiseriate rays 55
Mutation 322

N

Nebraska sandhills, vegetation of 532
Nilsson, H. H., work of 453
Noack, K., work of 88
North American flora 450

O

Oenothera, crosses of 191; cruciate-flowered 191; ovata, variation in 376; work with 455
Ohio, plants of 456
Oogenesis in Hormosira 264
Orchids, of Java 456; of oriental tropics 284
Orr, M. Y., work of 455
Osmunda, pith of 192
Osmundaceae, Jurassic 536
Osterhout, W. J. V. 178, 272, 367
Otis, C. H. 457

P

Panama, flora of 376
Parrott, P. J., work of 94
Pascher, A., "Die Süsswasser-Flora" 189
Peirce, G. J. 101
Peperomia, embryo sac of 374
Permeability 257
Persidski, D., work of 375
Phyllocrater 282
Piper, C. V., work of 192
Plant breeding in Sweden 453
Polygonatum commutatum, embryo sac of 143
Pool, R. J., work of 532, 533
Porodko, Th. M., work of 90
Porto Rico, climbing bamboos of 277
Praeger, R. L., "Weeds" 189
Prairie vegetation 377
Preissia, mitosis in 452
Prothallia, development of 99

Q

Quercus alba, anatomy of 53; rubra, anatomy of 50; virginiana, anatomy of 53

R

Rankin, W. M., work of 535
Ranunculaceae, embryogeny of 284
Reed, H. S., "Manual of bacteriology" 529
Reproduction in plants 337

Reviews: Baumann's "Die Vegetation des Untersees" 449; Benecke's "Morphologie und Entwickelungsgeschichte" 86; Grove's "The British rust fungi" 187; Hausrath's "Pflanzengeographische Wandlungen" 531; Hawley's "Forestry in New England" 188; Lock's "Rubber and rubber-planting" 188; Massart's "Nos arbres" 532; Paschers' "Die Süsswasser-Flora" 189; Praeger's "Weeds" 189; Reed's "Manual of bacteriology" 529; Rosenvinge's "The botany of Iceland" 530; Strasburger's "Die Kultur der Gegenwart" 86; Wernham's "The genus Sabicea" 189
Riss, Marie-Marthe, work of 89
Roberts, Edith A. 432
Roots, thermotropism of 254
Rosenvinge, K. L., and Warming, E., "The botany of Iceland" 530
Rubber 188

S

Sabicea 189
Sakamura, T., work of 372
Sand dune, a Welsh 455
Sandhills, vegetation of 532
Schaffner, J. H., work of 456
Schizocotyly 283
Scirpus validus, diaphragms of 495
Seedling anatomy 376
Seeds, germinating power of 101
Sex and chromosomes 454
Sexual fusions in aecidium 15
Sharp, L. W. 373, 419, 452, 453; work of 373
Shive, J. W., work of 281
Shull, G. H., work of 454
Sigmatochilus 282
Sinnott, E. W. 36; work of 536
Skottsberg, C., work of 96, 97, 190
Smilacina amplexicaulis, embryo sac of 140; sessifolia, embryo sac of 139
Smith, J. J., work of 284, 456
Snow, Laetitia M. 495
Soil moisture and evaporation 193
Souéges, R., work of 284
Spalding, E. S., work of 534
Spermatogenesis, in Marsilia 419
Spore conditions in hybrids 322
Sporogenesis in Equisetum 373
Standley, P. C., work of 376
Stewart, A., work of 94
Stopes, Marie C., work of 375
Strasburger, E., "Die Kultur der Gegenwart" 86
Streptopus roseus, embryo sac of 141
Subantarctic vegetation 96
Suspended vitality 375
Sweden, plant breeding in 453
Swingle, W. T., work of 192
Symphyogyna aspera, morphology of 401
Syncotyly 283
Synergids, fertilization of 375

T

Tansley, A. G., work of 535
Tetraspora, mitosis in 452
Thaxter, R. 235, 353
Thermotropism of roots 254
Tissues, killing by low temperature 451
Transeau, E. N. 282; work of 456
Transpiration of emersed water plants 457
Trifolium hybridum, morphology of 159; pratense, morphology of 156; repens, morphology of 160
Triggerson, C. J., work of 94
Tropisms, recent work on 88
Tyloses 283

V

Van Tieghem, Ph., sketch of 527
Vavilov, N. I., work of 455
Vestal, A. G. 377
Vicia americana, morphology of 161; mitosis in 372

W

Wager, H. A., work of 284
Washington, flora of southwestern 192
Water-balance of desert succulents 534
Weeds 189
Welwitschia 536
Wernham, H. F., "The genus Sabicea" 189
Wieland, G. R., work of 455
Wildeman, E. de, work of 284
Wilting coefficient 280
Winton, Kate B. 445

Y

Yapp, R. H., work of 450